

FOSSIL PONTOPORIID DOLPHINS (MAMMALIA: CETACEA) FROM THE PACIFIC COAST OF NORTH AMERICA

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ABSTRACT. Some remarkably long-snouted fossil marine odontocete cetaceans of late Tertiary age from the eastern margin of the North Pacific Ocean comprise an extinct group classified as the subfamily Parapontoporiinae of the family Pontoporiidae. These fossil dolphins belong in the genus *Parapontoporia* Barnes, 1984, which now includes three known species: latest Miocene *Parapontoporia pacifica* Barnes, 1984, from Baja California, Mexico; latest Miocene *P. wilsoni*, new species, from central California, U.S.A.; and Late Pliocene *P. sternbergi* (Gregory and Kellogg, 1927), from southern California. Analysis of the morphology of these animals indicates that they are closely related to species that have been previously classified in two separate living families of dolphins: the marine Pontoporiidae of the southwest Atlantic Ocean, and the freshwater Lipotidae of China.

The living pontoporiid, the La Plata dolphin or franciscana, *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844), lives in shallow water off the Atlantic coast of South America. It is apparently most closely related to two fossil Pliocene marine species, *Pontistes rectifrons* (Bravard, 1884) from Argentina and *Pliopontos littoralis* de Muizon, 1983, from Peru, and together these comprise the nominate subfamily Pontoporiinae of the Pontoporiidae. The name-bearer of the Lipotidae, the beiji or white flag dolphin, *Lipotes vexillifer* Miller, 1918, inhabits Tungting Lake and the Yangtze River (Chang Jiang) in China. This species was traditionally classified in the family Iniidae with the living Amazon dolphin or boto, *Inia geoffrensis* (de Blainville, 1817), and some fossil taxa, until 1979 when it was placed in the monotypic new family Lipotidae.

The fossil species in the subfamily Parapontoporiinae are intermediate morphologically and zoogeographically, however, between *L. vexillifer* and the species in the subfamily Pontoporiinae, and separate family status for *L. vexillifer* is therefore unwarranted. Based on the new information from the fossil record I recognize, at a new rank and in a new context, a third subfamily in the family Pontoporiidae, the Lipotinae.

INTRODUCTION

Four living genera of odontocetes in the superfamily Platanistoidea contain long-snouted species that are sometimes (although not in every case correctly) referred to as "river dolphins." *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844), the franciscana or La Plata dolphin, is a near-shore marine species living in the Atlantic Ocean off the coasts of

Brazil, Uruguay, and Argentina. *Inia geoffrensis* (de Blainville, 1817), the boto or Amazon dolphin, is a freshwater species living in the Amazon, Orinoco, and Madeira River systems of South America. *Lipotes vexillifer* Miller, 1918, the Beiji or white flag dolphin, is a freshwater dolphin inhabiting the Yangtze (Chang Jiang) River system (including Tungting Lake) and the Quiantang River system in China. *Platanista* spp., the susus or Ganges and Indus dolphins of India, Pakistan, Bangladesh, and Nepal are freshwater species.

Each of these four Recent genera has been designated as the type of a separate platanistoid family, although in most published works they have been classified in various subfamilies within the family Platanistidae (e.g., Flower, 1869; Simpson, 1945; Fraser and Purves, 1960). *Pontoporia* Gray, 1846, and *Platanista* Wagler, 1830, have usually been classified in their nominate subfamilies, but following Miller (1918, 1923), most zoologists have joined *Lipotes* Miller, 1918, and *Inia* d'Orbigny, 1834, in the family Iniidae or the subfamily Iniinae, depending on whether the Platanistoidea or Platanistidae was used as the next higher category (see Simpson, 1945; Brownell and Herald, 1972). Some authors have also classified *Pontoporia* within the Delphinidae (Gill, 1872; True, 1908; Miller, 1923; Kellogg, 1928), but they have been in the minority. Zhou, Qian, and Li (1979) recognized substantial differences between *Inia* and *Lipotes* and proposed a separate new family, the Lipotidae. Several fossil species, virtually all of them marine, have been reported to be relatives of various of these, and the systematics of the fossil and Recent Platanistoidea have had a convoluted and confusing history (Kellogg, 1928).

In recent years a larger number of cetologists and paleontologists have realized that the platanistoid dolphins are morphologically diverse and represent more than one family. For example, Kasuya (1973) recognized three extant families (Platanistidae, Iniidae, and Pontoporiidae) and Zhou (1982) recognized four, including the family Lipotidae. Both of these

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authors classified all of these families in the superfamily Platanistoidea, so that the hierarchical relationships among the groups remained virtually unchanged.

The purpose of this paper is to describe, diagnose, and analyze fossils of extremely long-snouted marine dolphins in the genus *Parapontoporia* Barnes, 1984, cetaceans that are morphologically similar to both *Pontoporia* and *Lipotes*. That *Parapontoporia* is morphologically intermediate between the Recent genera *Pontoporia* and *Lipotes* is important to systematics because, as mentioned above, *Pontoporia* and *Platanista* have usually been considered to be more remotely related to *Inia* and *Lipotes* than the latter were to one another.

The fossils that I describe in this study include those of *Parapontoporia pacifica* Barnes, 1984; *P. sternbergi* (Gregory and Kellogg, 1927); and *P. wilsoni*, new species, that were collected from latest Miocene and Late Pliocene sedimentary rock units bordering the eastern North Pacific Ocean in California and Baja California. The type species of *Parapontoporia*, *P. pacifica*, was based on a fossil from latest Miocene rocks, approximately 6 to 8 million years old, on Isla Cedros, Baja California, Mexico. I have previously demonstrated (Barnes, 1984) that *P. pacifica* is congeneric with *Stenodelphis sternbergi* Gregory and Kellogg, 1927, a species that is known from the Late Pliocene age San Diego Formation in California and one that had needed a new generic allocation for many years (see Barnes, 1973a, 1977). The geographic distribution of these fossils has important biogeographic implications because they are roughly equidistant between the areas occupied by *Lipotes vexillifer* and *Pontoporia blainvillei*. These specimens and taxa were included in a Ph.D. dissertation that I submitted to the University of California at Berkeley (Barnes, 1972), and some were subsequently mentioned in four following publications (Barnes, 1973a, 1977, 1983, 1984). In a subsequent study, Robert L. Brownell, Jr., Edward Mitchell, and I plan to review all fossil and Recent Pontoporiidae of the world and their interrelationships.

MATERIALS AND METHODS

Fossil specimens described in this study are conserved in scientific institutions in the United States as indicated by the following acronyms:

AMNH	American Museum of Natural History, New York, New York.
LACM	Natural History Museum of Los Angeles County, Los Angeles, California.
SDSNH	San Diego Society of Natural History, Natural History Museum, San Diego, California.
UCMP	University of California Museum of Paleontology, Berkeley, California.
UCR	University of California at Riverside, Department of Geological Sciences, Riverside, California.

Precise locality descriptions are not given for some of the specimens. Such information is available to qualified investigators upon request to the appropriate institution.

Comparative specimens of the modern species, *Pontoporia blainvillei*, *Lipotes vexillifer*, *Inia geoffrensis*, and *Platanista*

gangetica, were studied and used in formulating the descriptions and diagnoses, which are based on cranial characters. Each of the three fossil species of *Parapontoporia* is known by incomplete skulls that do not exhibit entirely overlapping morphology, but enough is known of each species to differentiate all three. The descriptions presented here do not duplicate those already published, but are written in a manner to avoid repetition. Measurements of the skulls were taken following the standardized methods outlined by Perrin (1975). Anatomical terminology for basicranial structures and the middle ear air sinus system follows Fraser and Purves (1960). Most other osteological terms follow Kernan (1918), Kellogg (1927), and Barnes (1978, 1984). All the rendered anatomical line drawings with line shading (Figs. 1a, 2a, 3a, 4, 10a, b, 11, 13, 15) were done by J. Patricia Lufkin using orthographic projection. My restorations of *Parapontoporia wilsoni* were derived from these. Specimens were coated for photography with a sublimate of ammonium chloride. My restorations of *P. sternbergi* are based on all available specimens from the San Diego Formation and on the type specimens of the other two species.

Anatomical structures in the illustrations are labeled according to the following abbreviations:

aon	—antorbital notch
Bs	—basisphenoid bone
ch	—cranial hiatus
fc	—carotid foramen
fh	—hypoglossal foramen
fio	—infraorbital foramen
fm	—maxillary foramen
fo	—foramen ovale
fp	—falcate process of the basioccipital
fpal	—palatine foramen
fpm	—premaxillary foramen
Fr	—frontal bone
gf	—glenoid fossa
jn	—jugular notch
Ju	—jugal bone
La	—lacrimal bone
mc	—maxillary crest
me	—maxillary eminence
Met	—mesethmoid bone
mf	—mental foramen
mrg	—mesorostral gutter
ms	—fossa for middle sinus
Mx	—maxillary bone
n	—naris
Na	—nasal bone
Oc	—occipital bone
occ	—occipital condyle
Pa	—parietal bone
Pal	—palatine bone
pop	—paroccipital process
Pmx	—premaxillary bone
Pt(II)	—pterygoid, lateral lamina
Pt(ml)	—pterygoid, medial lamina
pts	—fossa for pterygoid sinus

s—mandibular symphysis
Sq—squamosal bone
sqf—squamosal fossa
Vo—vomer bone

Some family group names have been used at various ranks. In cases where I recognize a revised rank, the original author is included in parentheses followed by the author of the emended rank that I recognize. All the variations and synonyms of the family- and genus-group names are listed in the synonymies.

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Superfamily Platanistoidea (Gray, 1863)
Simpson, 1945

Family Pontoporiidae (Gill, 1871)
Kasuya, 1973

Pontoporiinae Gill, 1871:124 (March, 1871), as a subfamily of Platanistidae; 1872:15, as a subfamily of Delphinidae.
Pontoporiadae Gray, 1871:95, incorrectly formed name, as a monotypic family for *Pontoporia* Gray, 1846.
Stenodelphininae True, 1908:391, as a subfamily of Delphinidae to include *Stenodelphis* d'Orbigny and Gervais, 1847, a junior synonym of *Pontoporia*.
Stenodelphininae. Miller, 1923:40, unjustified emendation of Stenodelphininae.
Pontoporiidae. Kasuya, 1973:28, 61, as a family of Platanistoidea.
Lipotidae Zhou, Qian, and Li, 1979:72, as a monotypic family for *Lipotes*.

DIAGNOSIS OF FAMILY. A family of Platanistoidea that differs from Platanistidae and Iniidae by having skulls with the following unique combination of characters: occipital shield roughly square in posterior view with prominent dorsolateral corners and not narrow dorsally, facial portions of maxillae relatively flat, not steeply inclined posteriorly or laterally, rostral portions of premaxilla and maxilla separated by longitudinal lateral groove, rostrum constricted transversely posterior to end of tooth row, posterior part of alveolar row located at lateral edge of palate and curving upward on side of rostrum at posterior extremity, palate nearly flat posterior to ends of alveolar rows, maxilla bearing a low, non-pneumatized crest over orbit which is oriented in an anterolateral to posteromedial direction and located medial to margin of maxilla rather than at the margin, fossa for pterygoid sinus having a branch extending dorsally adjacent to anterior wall of each naris, nares of small diameter and curving around anterior wall of braincase rather than being nearly vertical, foramen ovale small, round, distinct from cranial hiatus, located on basisphenoid bone on ventrolateral

wall of cranium and confluent with deep sulcus marking course of mandibular division of trigeminal nerve, zygomatic process of squamosal elongate, tapered, inclined anteriorly with large, transversely oriented postglenoid process, and prominent, anteroposteriorly oriented fossa curving around medial and posterior side of glenoid fossa for middle sinus of air sinus system, paroccipital process with fossa on side facing cranial hiatus that held posterior sinus of air sinus system, carotid foramen in basioccipital vestigial, periotic and bulla not firmly attached to braincase by posterior processes and accessory ossicles, teeth comparatively homodont with crowns having a lingual protuberance and roots having a swelling below the enamel line.

INCLUDED SUBFAMILIES. Parapontoporiinae Barnes, 1984; Pontoporiinae (Gill, 1871) Kasuya, 1973; and Lipotinae (Zhou, Qian, and Li, 1979), new rank and new context.

Subfamily Parapontoporiinae Barnes, 1984

Parapontoporiinae Barnes, 1984:6.

EMENDED DIAGNOSIS OF SUBFAMILY. A subfamily of Pontoporiidae differing from Pontoporiinae and resembling Lipotinae by having skull with cranial vertex asymmetrical and offset to left side, vomer exposed between maxillae on palate, spiracular plate on premaxillary surfaces flat, not elevated and convex, posterior terminations of premaxillae not widely separated from anterolateral corners of nasals, squamosal fossa between zygomatic process and braincase deep; resembling Pontoporiinae and differing from Lipotinae by having skull with extremely long, slender rostrum and mandible, very deep lateral groove between rostral parts of maxilla and premaxilla, lateral lamina of pterygoid joined with posterior plates of maxilla and palatine to form extensive bony wall within orbit (but not connecting posteriorly with basisphenoid as in *Pontoporia blainvillei*), tooth crowns small, sharply pointed, with basal lingual bulge, compressed anteroposteriorly and covered with smooth enamel, tooth roots flattened labio-lingually with encircling swelling at gum line; and differing from both Pontoporiinae and Lipotinae by having extreme polydonta, bearing 80 to 82 teeth in each side of each jaw (in contrast to 48 to 61 in *Pontoporia blainvillei* and 32 to 36 in *Lipotes vexillifer*).

INCLUDED GENERA. *Parapontoporia* Barnes, 1984 only.

Parapontoporia Barnes, 1984

Stenodelphis (part). Gregory and Kellogg, 1927.
“*Stenodelphis*.” Barnes, 1973a:37–39; 1977:333–334; Barnes, Howard, Hutchison, and Welton, 1981:56, 57, 61, 64; Deméré, 1981:24–25; de Muizon, 1983:1103.
Stenodelphininae, genus (and species) new. Barnes, 1977:331.
Parapontoporia Barnes, 1984:6.

DIAGNOSIS OF GENUS. Because the subfamily Parapontoporiinae is at present monotypic, the diagnosis for it and the genus *Parapontoporia* are identical.

TYPE SPECIES. *Parapontoporia pacifica* Barnes, 1984; type by original designation.

INCLUDED SPECIES. *Parapontoporia sternbergi* (Gregory and Kellogg, 1927); *Parapontoporia pacifica* Barnes, 1984; and *Parapontoporia wilsoni*, new species.

Parapontoporia pacifica Barnes, 1984

Figures 1–5, 20a, d

Stenodelphininae, genus and species new (part). Barnes, 1977: 331.

Parapontoporia pacifica Barnes, 1984:7.

EMENDED DIAGNOSIS OF SPECIES. A species of *Parapontoporia* differing from *P. wilsoni*, new species, and *P. sternbergi* by having skull with dorsal premaxillary surfaces at proximal end of rostrum flat-lying, not tilting medially to form a basin, and by having more elongate fossa for pterygoid sinus in palatine; and differing from *P. sternbergi* by lacking well-defined grooves on the lateral surfaces of dentaries, instead, nutrient foramina on lateral surface of dentary open into only a shallow, elongate depression.

HOLOTYPE. UCR 21244, skull with teeth, lacking the braincase and part of the facial region, mandible lacking right condyle and the post-alveolar section of the left dentary, a probable fifth cervical vertebra, and a first left rib; collected by David P. Whistler, 9–11 August 1965.

TYPE LOCALITY. UCR RV-6505 in weathered badlands exposures southeast of the village of Cedros on Isla Cedros, Baja California, Mexico.

FORMATION AND AGE. From the lower member of the Almejas Formation (Kilmer, 1979), latest Miocene, correlated indirectly with the “Jacalitos” provisional mega-invertebrate stage and the Hemphillian North American land mammal age, and approximately 6 to 8 million years old. The age of the lower member of the Almejas Formation has been discussed by Barnes (1973b, 1977, 1984) and Repenning and Tedford (1977). The Almejas Formation is approximately 800 feet thick and directly overlies the Middle Miocene age Tortuga Formation (Kilmer, 1977, 1979). Fossil invertebrate assemblages from the upper member of the Almejas Formation are similar to those from the Late Pliocene San Diego Formation and are therefore correlative with the “San Joaquin” provisional mega-invertebrate stage and the Blancan North American land mammal age. The vertebrate fossils in the lower member of the Almejas Formation on Isla Cedros are stratigraphically below the invertebrate fossils, in the basal approximately 130 feet of the formation.

The holotype of *Parapontoporia pacifica* was found five feet above the base of the Almejas Formation. Howard (1971) reported seven species of birds, Repenning and Tedford (1977) described walrus and a fur seal, and Barnes (1973b, 1977, 1984) reported 11 species of cetaceans from the lower member of the formation, mostly from horizons above that which produced *P. pacifica*.

The relatively diverse aggregate assemblage of published fossil vertebrate species from the lower member of the Almejas Formation warrants being listed here:

Aves

Puffinus tedfordi Howard, 1971

Puffinus sp.

Morus sp.

?*Megapaloelodus opsigenus* Brodkorb, 1961

Cerorhinca minor Howard, 1971

?*Endomychura* sp.

Mancalla cedrosensis Howard, 1971

Mammalia

Dusignathus santacruzensis Kellogg, 1927

Aivukus cedrosensis Repenning and Tedford, 1977

Thalassoleon mexicanus Repenning and Tedford, 1977
cf. *Plesiocetus* sp.

Balaenoptera sp.

Parapontoporia pacifica Barnes, 1984

Denebola brachycephala Barnes, 1984

Piscolithax tedfordi Barnes, 1984

Piscolithax boreios Barnes, 1984

Phocoenidae, gen. and sp. undetermined

Albireo whistleri Barnes, 1984

Delphinoidea, gen. and sp. undetermined

Praekogia cedrosensis Barnes, 1973

Physeterinae, gen. and sp. undetermined

DESCRIPTION. Skull. The skull (Figs. 1–3) of the holotype and only known specimen of *Parapontoporia pacifica* was described by Barnes (1984) and compared with several specimens of *P. sternbergi* from the younger, Late Pliocene age San Diego Formation. The relatively complete referred specimens of *P. sternbergi* described in the following text confirm that the two species are congeneric. The description of the skull of *P. pacifica* need not be repeated here, but I will summarize some of the main differences between it and the other species of *Parapontoporia*. The holotype of *P. pacifica* does not include the posterior part of the braincase, but it has the most complete rostrum of any known specimen of the genus. No available specimen of *P. sternbergi* has the tip of the rostrum preserved.

Some of the lateral lamina of the pterygoid of *P. pacifica* is preserved, and in company with a small posterior extension of the palatine and a larger projection of the maxilla, produces a thin wall of bone that extends posteriorly within the orbit (Fig. 2). This wall of bone spreads dorsally and partly obscures the foramina and sinuses on the medial wall of the orbit, but it does not appear to have reached posteriorly as far as the basisphenoid as it does in *Pontoporia blainvillei*. This is the only specimen of *Parapontoporia* in which any part of the lateral lamina of the pterygoid is preserved.

The groove on the lateral side of the rostrum that separates the premaxilla from the maxilla is not as deep as in *P. sternbergi*. The groove becomes increasingly wider and shallower distally, and at the anterior end of the rostrum the maxilla is fused to the premaxilla with no visible suture. Both *P. sternbergi* and *P. wilsoni*, new species, have a medial basin formed on the dorsal surface of the proximal part of the rostrum just anterior to the level of the antorbital notches. In *P. pacifica*, there is no such basin because the premaxillae are nearly flat-lying in that area, but both their medial and

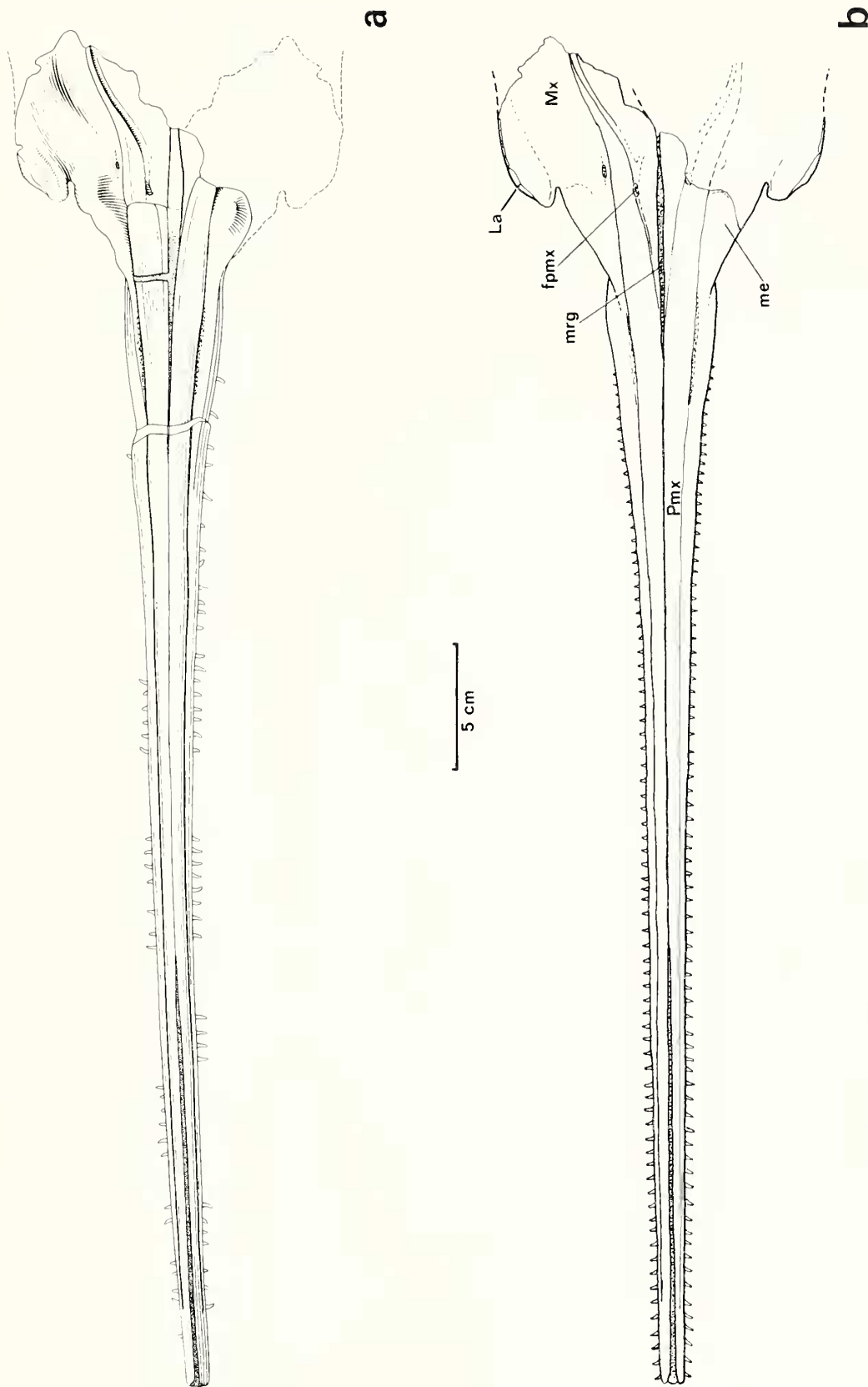
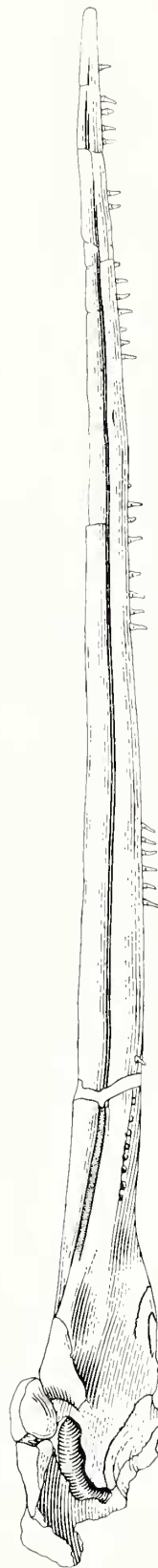
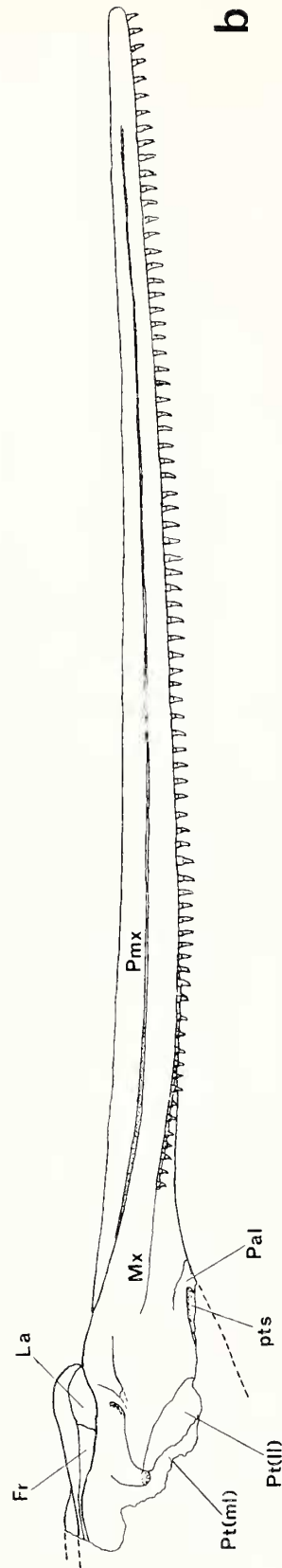


Figure 1. *Parapontoporia pacifica* Barnes, 1984, holotype, UCR 21244, partial skull, dorsal view: **a**, drawing of original specimen; **b**, restoration with structures labeled. Abbreviations used in this and the following illustrations are explained in the section titled Materials and Methods.



a

5 cm



b

Figure 2. *Parapontoporia pacifica* Barnes, 1984, holotype, UCR 21244, partial skull, right lateral view: a, drawing of original specimen; b, restoration with structures labeled.

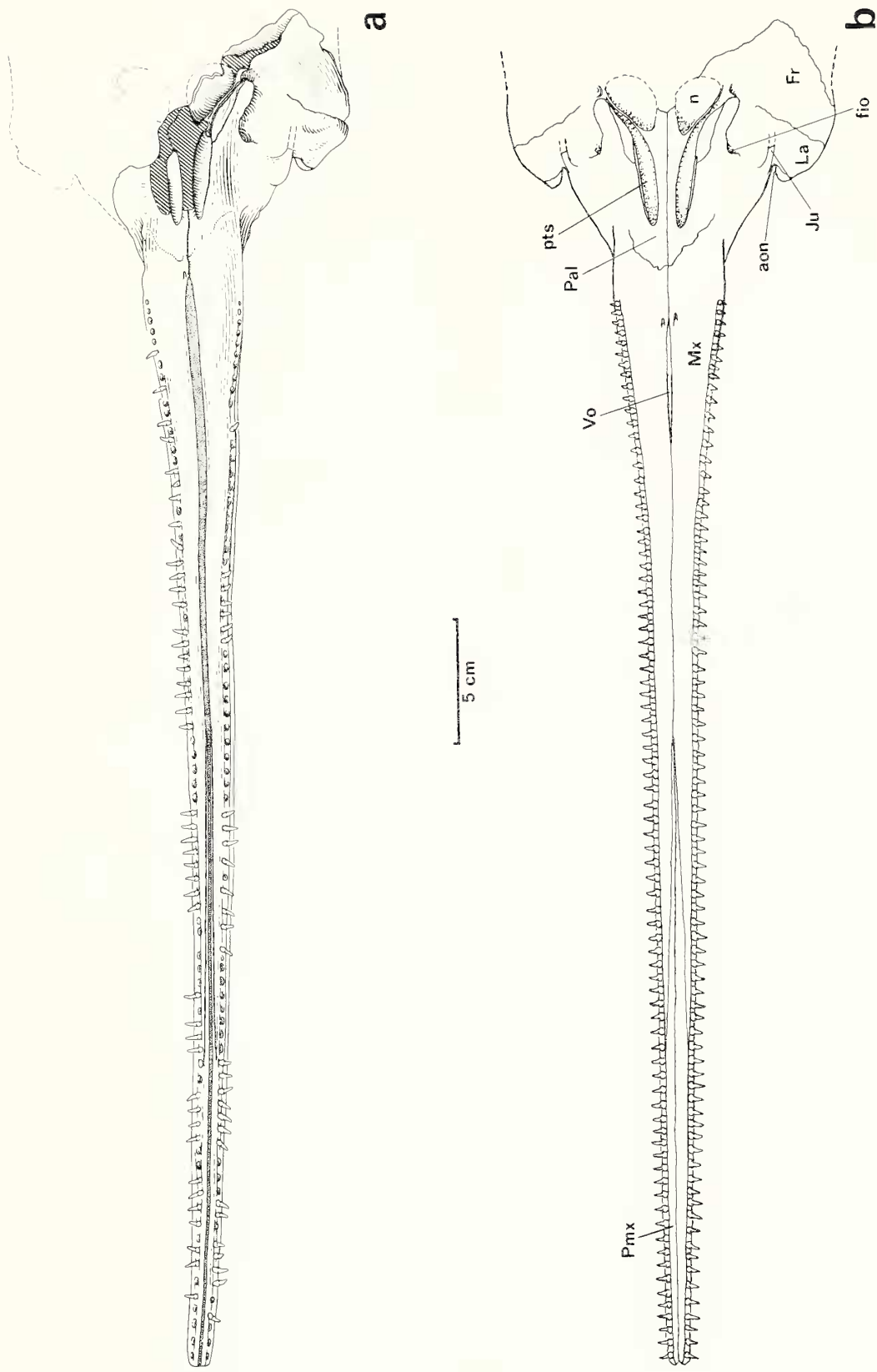


Figure 3. *Parapontoporia pacifica* Barnes, 1984, holotype, UCR 21244, partial skull, ventral view: a, drawing of original specimen; b, restoration with structures labeled.

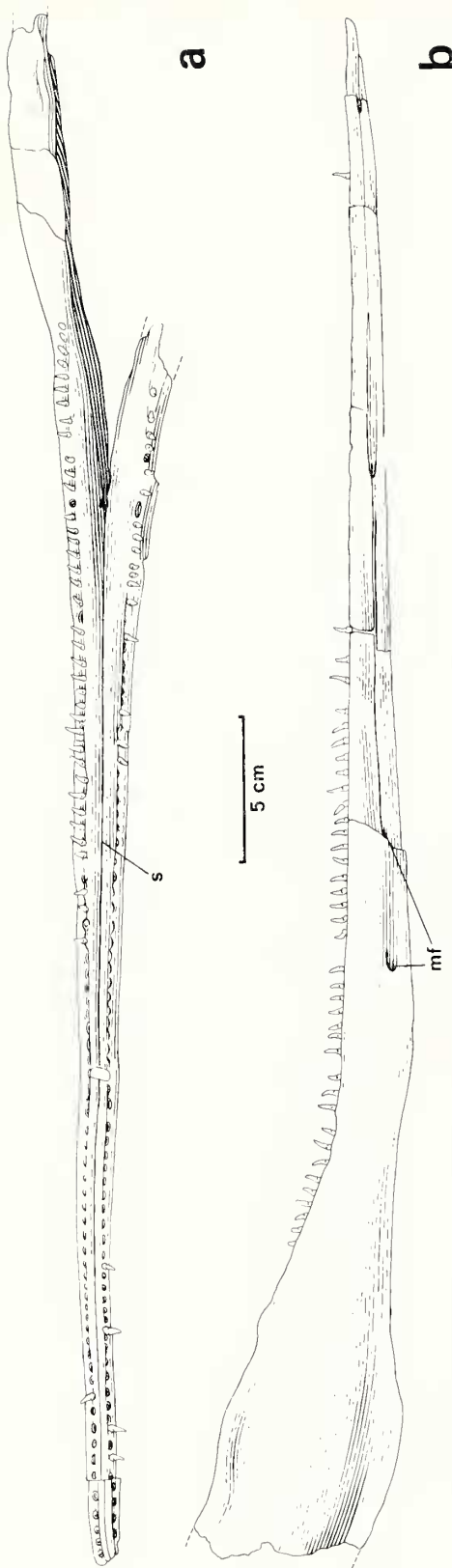


Figure 4. *Parapontoporia pacifica* Barnes, 1984, holotype, UCR 21244, partial mandible: a, dorsal view; b, right lateral view.

lateral margins are very slightly upturned (Figs. 20a–c). At this location there is no narrowing of the premaxillae as in *P. wilsoni*, new species.

The fossae in the palatine bones that held the pterygoid air sinuses are as long anteroposteriorly as in *P. sternbergi*, and nearly twice the length of those in *P. wilsoni*, new species. The rostrum had approximately 80 teeth on each side.

Mandible. The mandible with the holotype of *P. pacifica* (Fig. 4) is the most complete known mandible of any species of *Parapontoporia*. The right and left dentaries each bore alveoli for approximately 82 teeth. The specimen shares characters with the holotype mandible (AMNH 21905) of *P. sternbergi* and is similar in general size and proportions. It has a firmly fused mandibular symphysis marked by a medial groove dorsally and ventrally. The mandible of *P. pacifica* differs from that of *P. sternbergi* by lacking a deep lateral groove (such as is present in Recent *Pontoporia blainvillei*), but has instead only an elongate shallow depression that extends the length of the symphyseal part of each dentary slightly below mid-height on the lateral side (compare Figs. 20d and e).

All bone surface of the mandible is dense and in its tooth-bearing parts the mandible is marked by faint linear striae. Between the alveolar row and the dorsal edge of the lateral groove, the surface of the dentary is bowed outward in cross section. The dorsal surface of each dentary between the midline and the alveolar row is arched transversely.

The ascending ramus has a thin, arched coronoid crest about mid-length, and this culminates posteriorly in an upturned coronoid process (Fig. 4b). Neither *Lipotes vexillifer* nor *Pontoporia blainvillei* has a coronoid crest and in both species the coronoid process projects more posteriorly than dorsally.

Teeth. The teeth of *Parapontoporia pacifica* are like those of *Pontoporia blainvillei* (Figs. 5a–d), but have relatively higher crowns. The smooth enamel crowns curve lingually, have a basal lingual bulge, and are compressed anteroposteriorly. The roots have a swelling encircling them at the gum line and are compressed labio-lingually. The anterior teeth have relatively slender, erect crowns, but progressing posteriorly the crowns are shorter and bend more medially. Because they are more bulbous, the crowns of the posterior teeth are not as compressed anteroposteriorly as are the ones of the more slender anterior teeth.

Cervical vertebra. One isolated vertebra (Fig. 5e), probably a fifth cervical vertebra, was associated with the holotype skull and mandible. This vertebra is greatly compressed anteroposteriorly, has a centrum that is nearly square in outline, a slender neural arch, small diapophyses and parapophyses, and a large transverse foramen that probably did not have a complete bony arch on its lateral side.

This vertebra resembles the fifth cervical of *Lipotes vexillifer* (Miller, 1918:pl. 12, the vertebra that is placed at lower left in the illustration) in having a low, broad neural canal, dorsoventrally expanded transverse foramen, and ventrally directed parapophyses. The resemblance of this vertebra to the fifth cervical of *Pontoporia blainvillei* is not so striking, because in that species (de Carvalho, 1961:fig. 11e) the bone

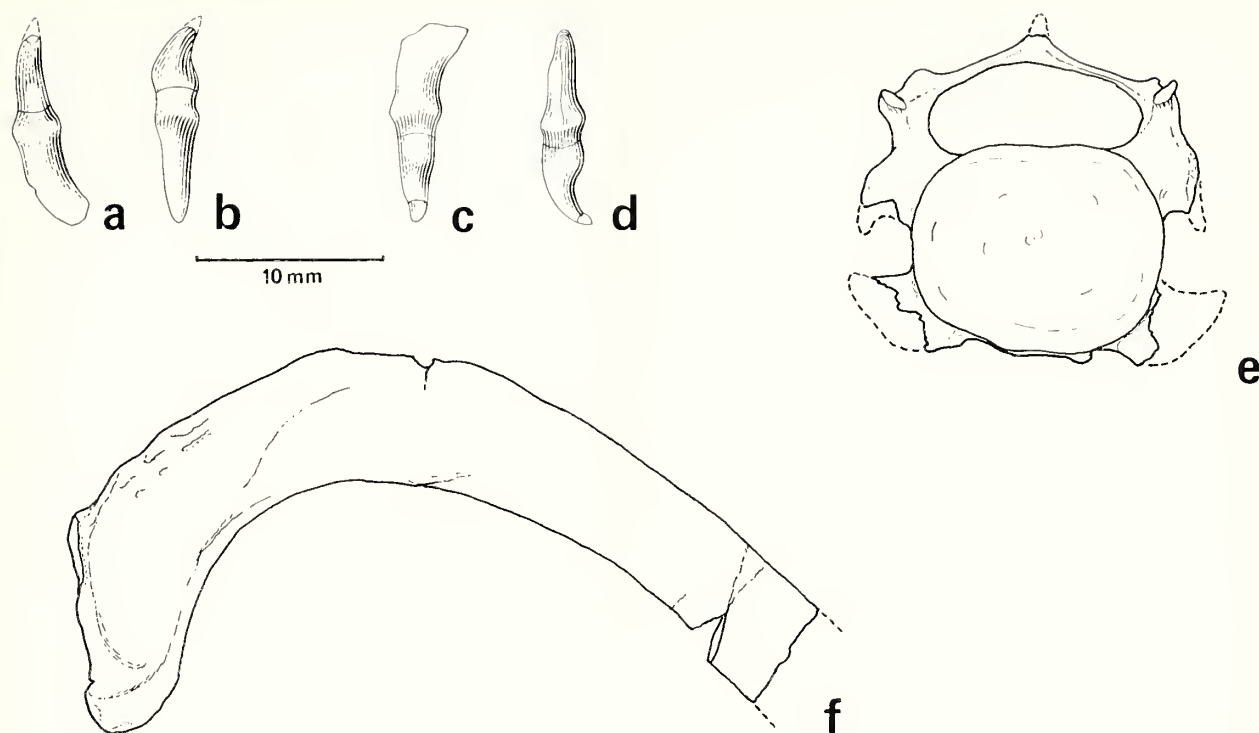


Figure 5. *Parapontoporia pacifica* Barnes, 1984, holotype, UCR 21244, right mandibular tooth: **a**, lingual view; **b**, anterior view; right maxillary tooth: **c**, lingual view; **d**, anterior view; **e**, cervical vertebra, anterior view; **f**, anterior right rib, anterior view. Scale line is for Figs. **a**–**d** only, Figs. **e**, **f** natural size.

has relatively larger diapophyses and parapophyses, a higher neural canal, a dorsoventrally compressed transverse foramen, a broader centrum, and no ventral extension of the parapophyses.

Rib. The proximal part of one rib (Fig. 5f), apparently a first left rib, belongs with the holotype. This rib has a large capitulum, a flat tuberculum, a short neck, a wide but anteroposteriorly compressed body, and is strongly curved at its proximal end.

Parapontoporia sternbergi
(Gregory and Kellogg, 1927)

Figures 6–10, 17b, 20c, e, 21b

Stenodelphis sternbergi Gregory and Kellogg, 1927:1.

“*Stenodelphis*” *sternbergi* Gregory and Kellogg, 1927. Barnes, 1973a:37–38; 1977:333–334; Barnes, Howard, Hutchison, and Welton, 1981:56, 57, 61, 64; Deméré, 1981:24–25; de Muizon, 1983:1103.

Parapontoporia sternbergi (Gregory and Kellogg, 1927). Barnes, 1984:6.

EMENDED DIAGNOSIS OF SPECIES. A species of *Parapontoporia* differing from *P. wilsoni*, new species, by having skull with facial region wider than long, antorbital processes larger, cranial vertex (comprised of frontals and nasals) higher and more compressed transversely, occipital

condyles projecting less prominently posteriorly from occipital shield, premaxillary surfaces forming less of a basin at proximal end of rostrum, nares passing more vertically through the skull, temporal fossa compressed anteroposteriorly with its height and length approximately equal, more elongate fossa for pterygoid sinus in palatine, zygomatic process of squamosal more inclined anteriorly, squamosal between postglenoid process and paroccipital process highly compressed anteroposteriorly; and differing from *P. pacifica* by having basin formed on premaxillary surfaces on proximal part of rostrum, shorter fossa for pterygoid sinus in palatine, and deeper groove on rostrum between maxilla and premaxilla, and by having mandible with deep groove on lateral side of each dentary.

HOLOTYPE. AMNH 21905, a section of mandible in the symphyseal area with 24 teeth which have badly eroded crowns, collected by John Reiland. The specimen is not a rostral fragment as was stated by Gregory and Kellogg (1927).

TYPE LOCALITY. India Street at West Walnut, San Diego, San Diego County, California.

REFERRED SPECIMENS FROM THE SAN DIEGO FORMATION. Nearly complete skulls, LACM 6238, SDSNH 22633, 23084; rostra lacking braincases, LACM 26605, SDSNH 25022; cranial vertices, LACM 58902, UCMP 129662, UCMP 129663; cranial vertex associated with rostral fragments, LACM 30464; right squamosal, LACM 26597; partial left maxilla, SDSNH 24794; cranial fragments, LACM

30465; periotics, LACM 58901, LACM 103975, SDSNH 20941, 23058, 23630, 23631, 24734, 25049, UCMP 88581, UCMP 88589, UCMP 129660, UCMP 129661; rostral fragments associated with mandible fragments and teeth, UCMP 88590; premaxillary fragment with teeth, UCMP 88588; rostral fragments, LACM 30432, LACM 30433, LACM 31065; nearly complete mandible, SDSNH 18671; and mandible fragments, LACM 26594, LACM 30463, LACM 30468, LACM 30471 (with teeth), LACM 30472, LACM 30475, LACM 30476, LACM 104004, UCMP 88587.

FORMATION AND AGE. Lower member of the San Diego Formation, Late Pliocene, correlated with the "San Joaquin" provisional mega-invertebrate stage of Addicott (1972) and the Blancan North American land mammal age, and therefore approximately 2 to 4 million years old. The fossil fauna and age of this rock unit have been discussed by Howard (1949), Hertlein and Grant (1954), Barnes (1973a, 1977:332–334), Repenning and Tedford (1977:69–70, fig. 6), and Deméré (1982, 1983).

DESCRIPTION. Skull. The rostrum, mandible, and teeth are the only anatomical parts shared in common between known specimens of *P. pacifica* and *P. sternbergi*, and the braincase and proximal part of the rostrum are the only parts shared in common between specimens of the latter species and *P. wilsoni*, new species. To avoid repetition, I shall emphasize in the following text those characters whereby *P. sternbergi* differs from *P. wilsoni*, new species, and *P. pacifica*, and those parts of the skull that are not known for *P. pacifica*.

The skull of *P. sternbergi* (Figs. 6–8) has a braincase that is somewhat square or boxy in its proportions and it has an extremely long and narrow rostrum. Many of the characters that separate *P. sternbergi* from *P. wilsoni*, new species, are related to the derived state of foreshortening or anteroposterior compression of the braincase of *P. sternbergi* (Fig. 21). This compression is the phenomenon termed telescoping by Miller (1923), whereby the crania of Cetacea have become modified from the condition in generalized mammals so that the bones extend anteroposteriorly past one another. In odontocetes, the predominance of posterior movement of the rostral bones toward the occipital region is typical, and in the more derived states, involved an anteroposterior compression of the braincase as well.

The braincase proportions of *P. sternbergi* are somewhat like those of Recent *Lipotes vexillifer* (Figs. 17b, c), but are different in details, both primitive and derived. The braincase is deep dorsoventrally and has a nearly vertical occipital shield and a wide and fairly flat facial surface that narrows abruptly at the juncture with the rostrum.

On the posterior part of the rostrum, the dorsal surfaces of the premaxillae slope medially toward the mesorostral gutter to form a central basin. At its deepest point, just anterior to the antorbital notches, this basin is approximately 5 mm lower than the adjacent maxillary surfaces (Fig. 20c). Progressing anteriorly from the basin the premaxillae gradually become less tilted. There is a triangular shaped rough area on each premaxilla anterior to the nares. In delphinoids this is the site of attachment of the nasal plug muscle (Lawrence and Schevill, 1956), and a similar situation undoubtedly

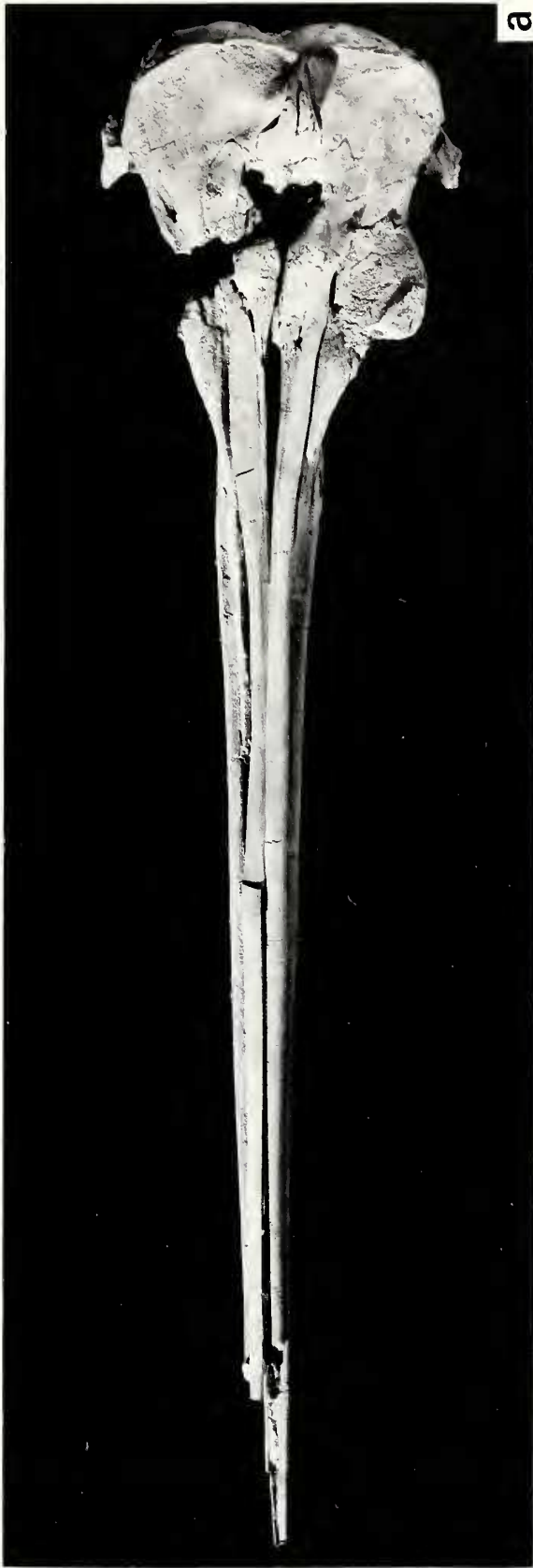
existed in *P. sternbergi*. The narrow anterior end of this rough area extends into the deepest part of the rostral depression (Fig. 6).

For most of their rostral length the premaxillae are slender, very dense and are separated from the maxillae by a deep longitudinal groove on each side (Fig. 7). There are no obvious maxilla-premaxilla sutures within these grooves. The premaxillae form most of the dorsal surface of the rostrum and roof over the mesorostral gutter, touching (but not fused) for much of their length at the midline. They extend to the extreme anterior tip of the rostrum, and are separated medially there for a short distance to expose the mesorostral gutter. Near the rostral basin the premaxillae become increasingly wider, the grooves between them and the maxillae disappear, and the premaxillae diverge to expose the mesorostral gutter.

At a point approximately 5 mm posterior to the antorbital notches, each premaxilla is perforated by a premaxillary foramen which, as in a common odontocete pattern, is connected to three sulci; anteromedial, posteromedial, and posterolateral. The anteromedial sulcus is partly roofed over by bone and defines the lateral margin of the narrow anterior extension of the rugose area of attachment of the nasal plug muscle (mentioned above). The posterolateral sulcus is deeply incised into the premaxilla. It diverges sharply away from the midline of the skull as it courses toward the lateral margin of the premaxilla, then continues posteriorly in a shallow groove on the maxilla following the edge of the premaxilla. The posteromedial sulcus branches off the posterolateral sulcus just posterior to the premaxillary foramen, but it is very shallow and extends only approximately 15 mm.

Beginning immediately anterior to the nares, the premaxillae become slightly elevated above the surrounding maxillae, and this condition persists to the posterior termination of each premaxilla. These elevated areas around the nares were smooth surfaced in life, but on either side of the available skulls the bone surface is now partly eroded away. When the animal was alive, these slightly elevated premaxillary surfaces, the spiracular plates, supported the premaxillary sacs (which are diverticula of the nasal passages, see Mead, 1975). These plates are asymmetrical. The one on the right side is wider and more elevated on its lateral edge than the one on the left. The left plate tilts more toward its lateral edge, and extends farther posteriorly. Each premaxilla terminates about 5 mm from the corresponding nasal. Extending posteriorly from the posterior end of each premaxilla there is a rough area on the maxilla indicating that at some previous point in the evolutionary history of this lineage of dolphin the premaxilla had extended farther posteriorly adjacent to the nasal as in, for example, the squalodonts.

The mesethmoid septum between the nares is canted to the left as it rises from the skull, and the left naris is slightly larger than the right. The basic construction of the bones surrounding the nares is very similar to that in *Lipotes vexillifer*, and is different from that in *Pliopontos littoralis* and *Pontoporia blainvillei*, in which the spiracular plates are more elevated and the bones around the nares are symmetrical (Fig. 17).



5 cm

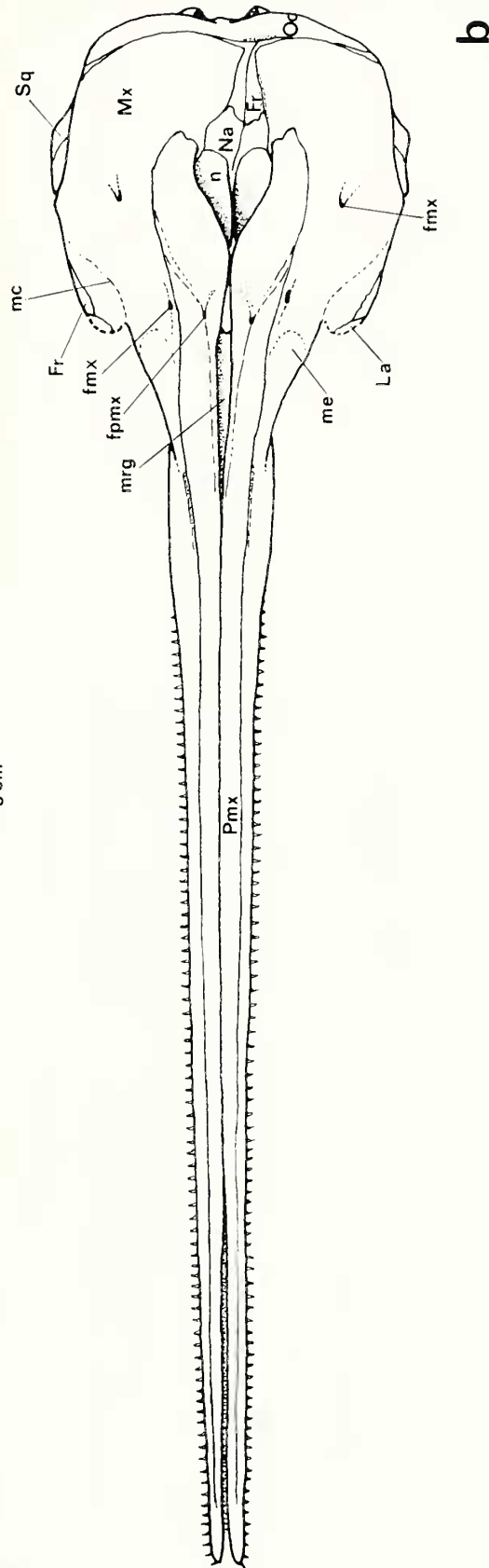


Figure 6. *Parapontoporia sternbergi* (Gregory and Kellogg, 1927), referred specimen, LACM 6238, skull, dorsal view: a, photograph of original specimen; b, restoration based on all known specimens of the species with extremity of rostrum based on *P. pacifica*.

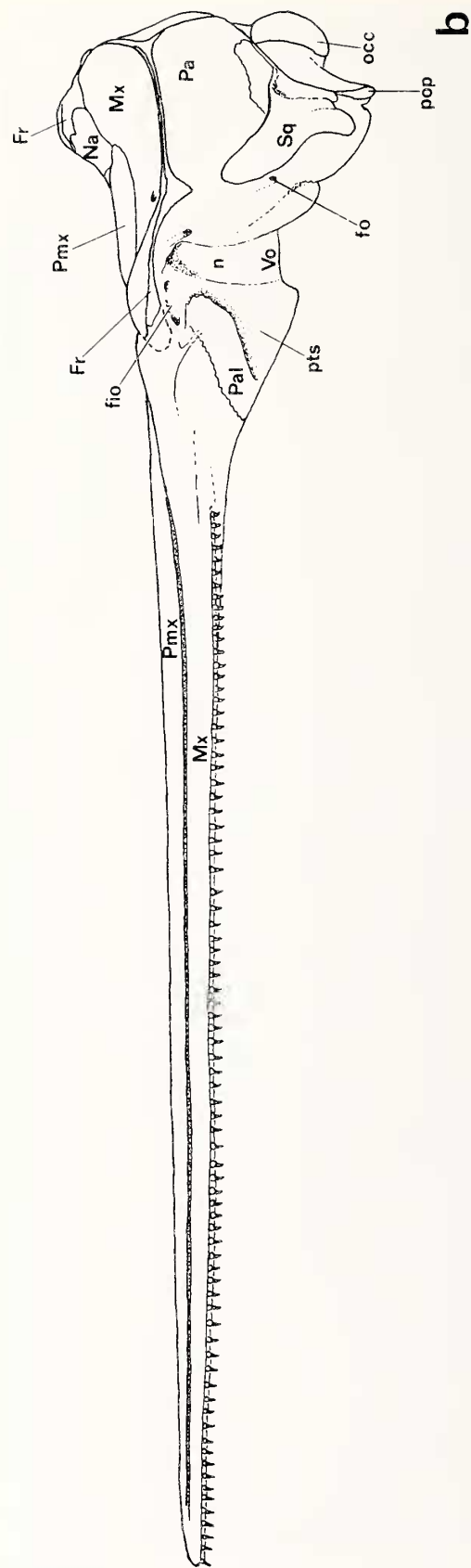
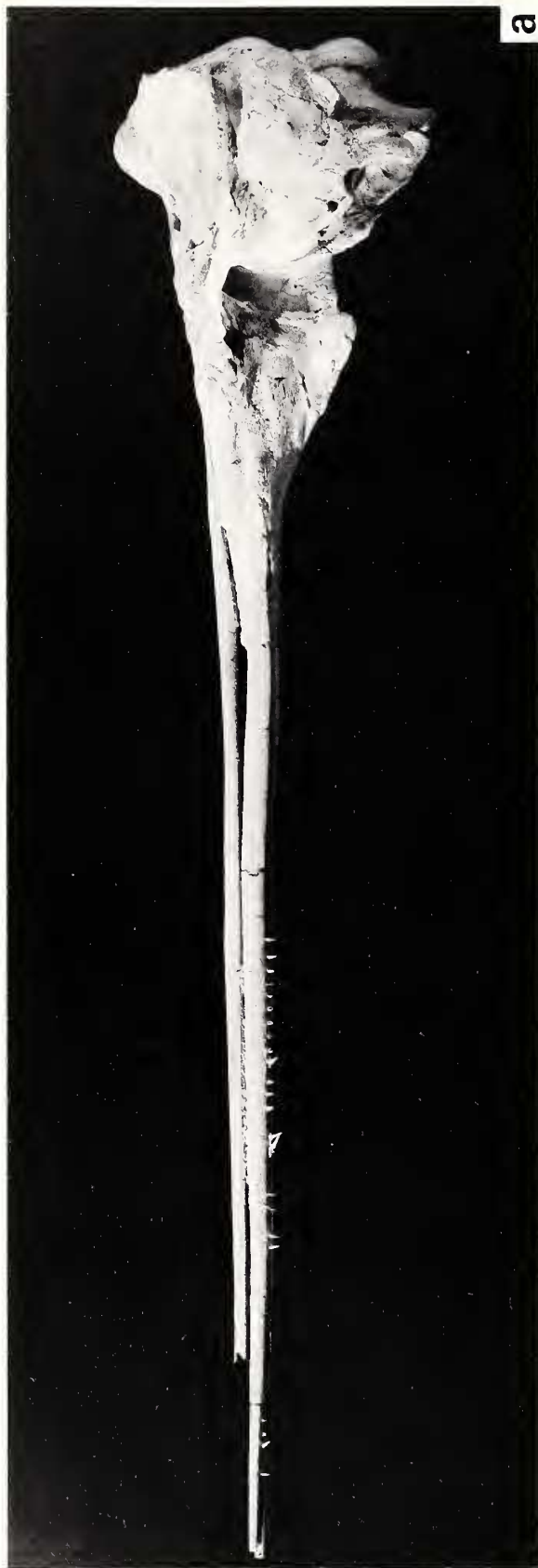


Figure 7. *Parapontoporia sternbergi* (Gregory and Kellogg, 1927), referred specimen, LACM 6238, skull, left lateral view: **a**, photograph of original specimen; **b**, restoration based on all known specimens of the species with extremity of rostrum based on *P. pacifica*.

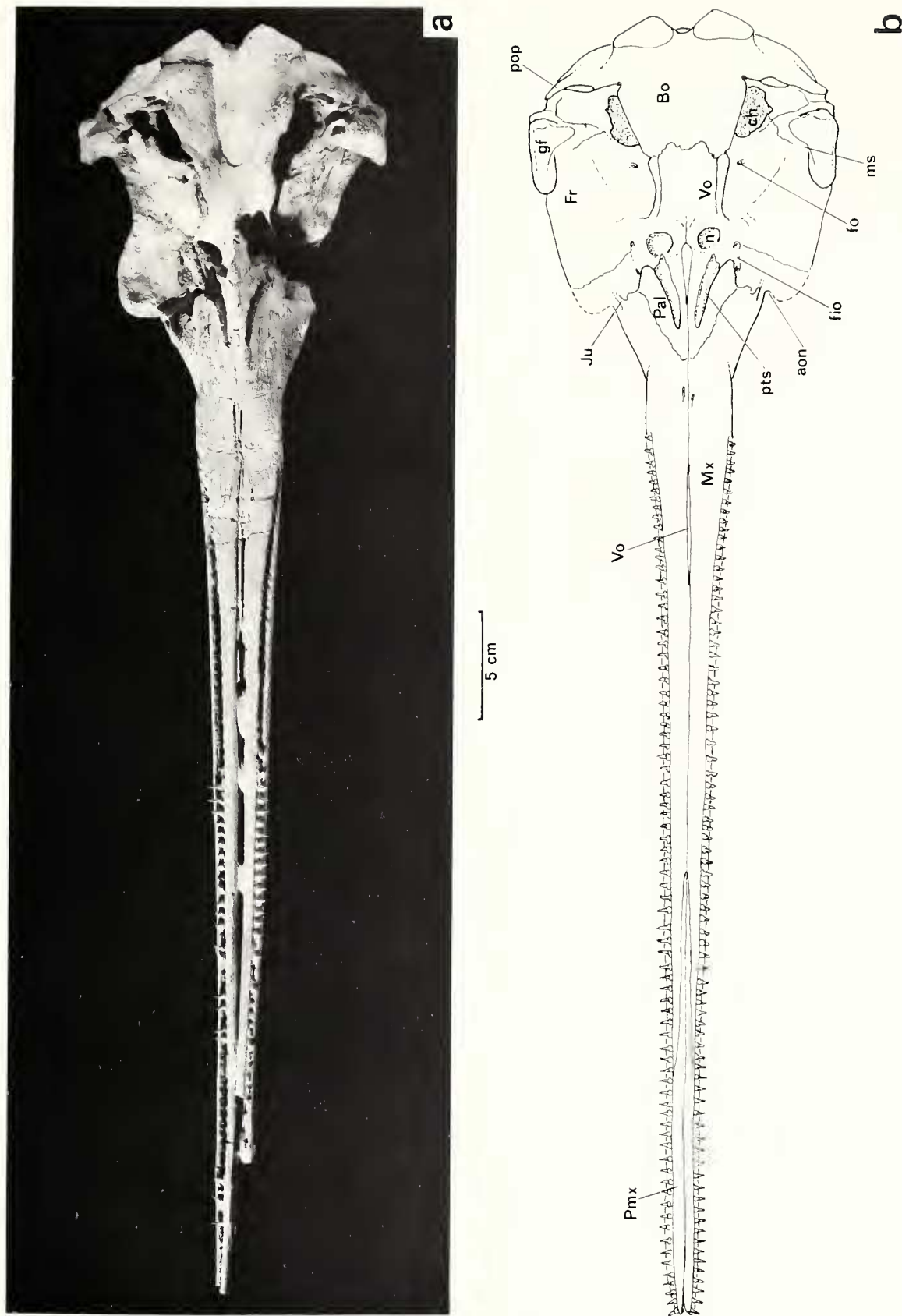


Figure 8. *Parapontoporia sternbergi* (Gregory and Kellogg, 1927), referred specimen, LACM 6238, skull, ventral view: a, photograph of original specimen; b, restoration based on all known specimens of the species with extremity of rostrum based on *P. pacifica*.

Table 1. Measurements (in mm) of skulls of *Parapontoporia*. Parentheses indicate estimated measurements. Method follows Perrin (1975).

	<i>P. pacifica</i>	<i>P. wilsoni</i>	<i>P. sternbergi</i>			
	UCR	UCMP	LACM	LACM	SDSNH	SDSNH
	21244	83790	6238	26605	22633	23084
Condylobasal length	—	—	(596+)	—	(605+)	—
Length of rostrum	477	—	(467+)	(341+)	(475+)	—
Width of rostrum at base	(80)	71	69	(64)	(64+)	(61+)
Width of rostrum at midlength	17	—	—	—	—	—
Width of premaxillae at midlength of rostrum	12	—	—	—	—	—
Greatest preorbital width	(126)	104	108	—	—	—
Greatest postorbital width	—	(124)	—	—	120	(118)
Least supraorbital width	(112)	113	—	—	—	—
Greatest width of external nares	—	33	31	—	26	26
Width across zygomatic processes of squamosals	—	138	141	—	(136)	—
Greatest width of premaxillae	—	58	58	—	50	(54)
Greatest parietal width within temporal fossae	—	106	109	—	98	—
Vertical external height of brain case	—	—	94	—	85	—
Internal length of brain case	—	—	94	—	—	—
Length of temporal fossa	—	(73)	—	—	(72)	—
Width of temporal fossa	—	(48)	—	—	41	—
Length of orbit	—	44	—	—	—	—
Length of antorbital process of lacrimal	22	22	—	—	—	—
Length of tooth row	414	—	(398+)	(282+)	(430+)	—

Like the premaxillae, the maxillae are for much of their rostral length composed of dense bone on both their labial and palatal surfaces. The rostrum is constricted transversely at a point approximately 50 mm anterior to the antorbital notches. Both *Lipotes vexillifer* and *Pontoporia blainvillei* have a similar constriction, and it is formed in the following manner. In this area the dense part of the maxilla which is lateral to the tooth row departs from the edge of the premaxilla and extends onto the ventrolateral edge of the rostrum. Posterior to this and anteromedial to the antorbital notches, the porous part of the maxilla is elevated into an eminence that swells dorsally and laterally. The tapered anterior end of this maxillary eminence extends anteriorly forming the lateral edge of the rostrum and passes dorsal to the posterior end of the dense section of the maxilla forming the tooth-bearing part of the rostral margin. This constriction of the margin of the rostrum is typical of all Pontoporiidae (Fig. 17).

The maxillary eminence has pushed the margin of the adjacent premaxilla medially and also constricts the anterior opening of the antorbital notch (Fig. 6). Posteromedial to each maxillary eminence is a single maxillary foramen which is confluent with shallow sulci running posteriorly and anteriorly from it, parallel to the margin of the premaxilla.

All known skulls of *P. sternbergi* have suffered breakage and/or abrasion of the supraorbital area so that details of the antorbital process and maxillary crest are not known for the species. From what is preserved, the species appears to be similar in these structures to *P. pacifica* and *P. wilsoni*, new

species, but to have had a more prominent antorbital process. There is an obliquely oriented maxillary crest over the orbit, and the skull SDSNH 22633 has the anterior end of the zygomatic process of the jugal located anteromedial to the antorbital notch (Deméré, 1981:fig. 9) as in the other two species. The same skull, illustrated by Deméré, has the best preserved postorbital process of the frontal of any specimen known of the genus. The process is short and broadly triangular, proportionally shorter and smaller than in *Pontoporia blainvillei*, and not slender with a distal rugosity as in *Lipotes vexillifer*. It apparently did not contact the tip of the zygomatic process of the squamosal (Fig. 7).

The posterior end of each maxilla wraps around the posterior side of each nasal and contacts the elevated frontal on the cranial vertex. In so doing, the maxillae encroach so far medially upon the frontals that just posterior to the cranial vertex only a 2-mm-wide exposure of frontals separates the right maxilla from the left. The cranial vertex is formed of the frontals and nasals and is in the form of an anteroposteriorly elongate, asymmetrical, slightly twisted knob with a cleft at the median suture on its anterior surface. Like the narial region, it is offset to the left side. The median suture between the right and left frontals on the cranial vertex is 13 mm to the left of the midline of the skull, as marked by the septum within the braincase that separated the cerebral hemispheres of the brain. The exposed frontals form the highest point of the vertex just posterior to the nasal bones, and there is a lower area between that point and the occipital crest. This low area posterior to the vertex exists also in other

Pontoporiidae and in Iniidae, and is unlike the condition in species of Delphinidae and Phocoenidae, in which the cranial vertex increases in height continuously from the nares to the occipital crest. Each nasal is thin and wraps around the steeply inclined anterior side of its corresponding frontal. The mesethmoid, forming the posterior walls of the nares, is inclined in the same plane as the nasals, from which it is separated by arcuate sutures.

The occipital shield is oriented almost vertically (Fig. 7), much as in *Lipotes vexillifer*. As in both *Pontoporia blainvillei* and *Lipotes vexillifer*, it is approximately square in posterior view, and adjacent to the temporal fossae its dorsolateral corners are prominent. As in *Pontoporia blainvillei*, the midline of the occipital shield is marked by a prominent median sulcus that extends from the apex of the foramen magnum dorsally to the occipital crest, and is flanked by a large, convex area on each side corresponding to the cerebral hemispheres of the brain. Each convex area is separated from the occipital condyle below it by a prominent oblique sulcus that is not present in *Pontoporia blainvillei*. The occipital condyles are moderately convex and set off prominently from the occipital shield. The dorsal margin of the foramen magnum forms a triangular peak somewhat like that in *Pontoporia blainvillei*. In *Lipotes vexillifer* the foramen magnum is more circular in shape.

The temporal fossa is open posteriorly and curves around the lateral side of the occipital shield. Dorsally, the facial parts of the maxilla and frontal project approximately 8 mm laterally over the posterior part of the temporal fossa. The squamosal fossa, which floors the temporal fossa, forms a deep recess between the cranium and the zygomatic process of the squamosal. Anteriorly the squamosal fossa is floored by only a thin shelf of bone spanning between the zygomatic process and the cranium.

The paroccipital process is located relatively far anteriorly on the braincase and therefore lies beneath the posterior end of the temporal fossa. The paroccipital process terminates ventrally in a flat, rugose surface and is separated medially from the falcate process of the basioccipital by a narrow, deep jugular notch. At the apex of this notch is a relatively large hypoglossal foramen that is nearly 3 mm in diameter.

The zygomatic process of the squamosal is deep and long, and its anterior end is upturned. There is a large, pointed, ventrally directed postglenoid process. The glenoid fossa is canted dorsomedially on the zygomatic process so that the external surface forms a flange which projects ventrolaterally. This ventrally projecting border is deepest anterior to the center of the glenoid fossa and posterior to the point where the zygomatic process turns upward. The glenoid fossa extends medially as a thin shelf which partly underlies a very large fossa for the middle sinus of the middle ear air sinus system. The fossa extends anteriorly along the medial side of the zygomatic process much as in *Lipotes vexillifer* and *Pontoporia blainvillei*. On its lateral surface the zygomatic process of the squamosal is excavated posteriorly by a rugose sternomastoid muscle fossa. The postglenoid process of the squamosal is close to the paroccipital process and there is much wrinkling and compression of the intervening bone,

including the muscle fossa, immediately dorsal to the external auditory meatus. Such extreme anteroposterior compression does not exist in this part of the squamosal in *P. wilsoni*, new species.

The cranial hiatus is the opening between the squamosal and the basioccipital in which the periotic lay and through which nerves and blood vessels passed, connecting the ear to the endocranial cavity. This hiatus in *P. sternbergi* is large (Fig. 8), but not relatively as large as in *Pontoporia blainvillei*. There is no indication that there was a large falciform process of the squamosal lateral to the hiatus such as is present in species of Delphinidae. A small falciform process is present in *Pontoporia blainvillei*. Large fossae in the bone around the cranial hiatus of *P. sternbergi* indicate the locations in life of extensive air sinuses. There was a large posterior sinus in the anterior wall of the paroccipital process. A much larger one occurs in the same location in *Pontoporia blainvillei*, and a smaller one exists in *Lipotes vexillifer*. The peribullary sinus in *P. sternbergi* extended laterally dorsal to the posterior process of the periotic, as well as medially where it occupied a large fossa in the lateral side of the falcate process of the basioccipital. The extent of excavation of the falcate process by this fossa is exceptional when compared to most other species of odontocetes, especially *Pontoporia blainvillei*, in which this process is very thick. At the front of this fossa, the very small carotid foramen pierces the basioccipital approximately 5 mm posterior to the suture between the pterygoid and the basioccipital. Lateral to this the basisphenoid bridges between the squamosal and the pterygoid, and bears the foramen ovale which is 4 mm in diameter and located approximately 8 mm anterior to the anterior margin of the cranial hiatus. A deep sulcus, marking the former course of the mandibular division of the trigeminal nerve, leaves the foramen ovale and extends posterodorsally across the basisphenoid (Fig. 8).

The medial lamina of the pterygoid forms a crest that is continuous with, but thicker than, the falcate process of the basioccipital. The posterior end of the vomer covers the ventral surface of the basisphenoid, spreads laterally to within 3 mm of the ventral edge of each pterygoid crest, and stops at the basisphenoid–basioccipital suture. Posteriorly, each falcate process of the basioccipital ends in a curved margin, and between that and the paroccipital process of the exoccipital the hypoglossal foramen lies at the apex of the jugular notch. In *Pontoporia blainvillei* the same foramen lies outside of, and posterior to the notch, rather than within it.

The anterolateral wall of the braincase is very well preserved only in LACM 6238. It is convex and remarkably devoid of foramina, sinuses, and bony processes or crests. The orbit is not as well preserved on any known specimens of *P. sternbergi* as it is on the holotype of *P. wilsoni*, new species, and the description of the latter species should, therefore, be consulted for data on the orbit of *Parapontoporia*.

The vomer forms a deep, narrow keel between the internal nares, and is continuous with the very deep, narrow keel formed by the palatines between the fossae for the pterygoid sinuses (Fig. 20c). These narrow fossae are closely appressed on either side of this very deep and narrow keel at the pos-

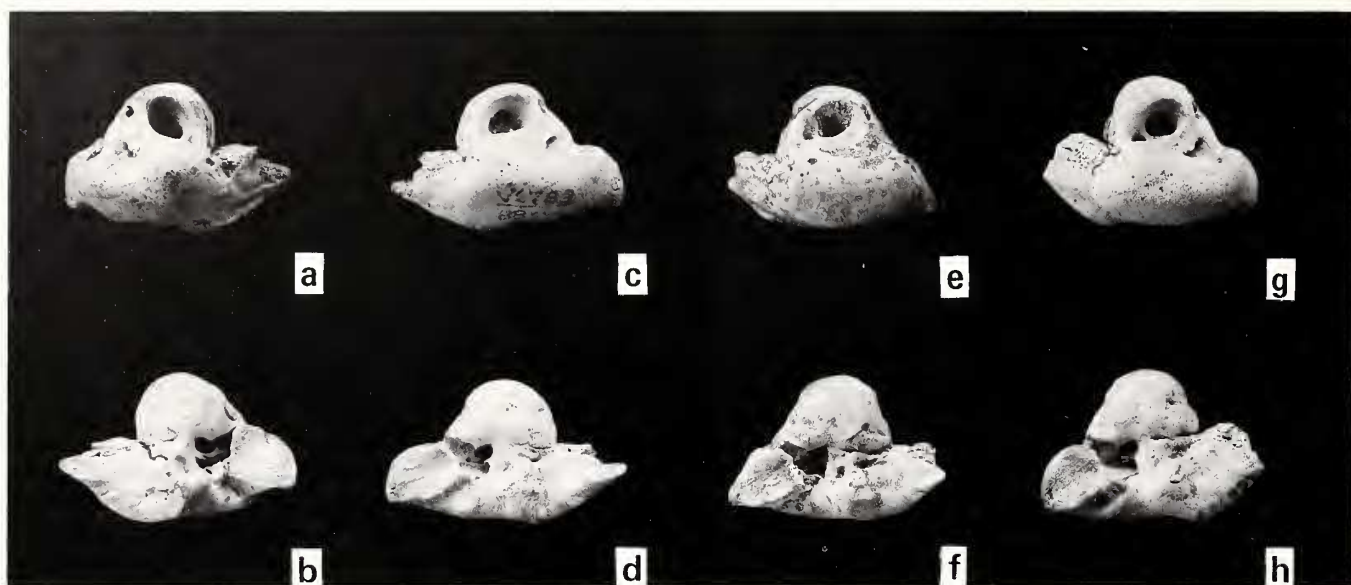


Figure 9. *Parapontoporia sternbergi* (Gregory and Kellogg, 1927), referred periotics from the San Diego Formation: UCMP 88581, right: a, cerebral view; b, tympanic view; UCMP 88589, left: c, cerebral view; d, tympanic view; LACM 58901, left: e, cerebral view; f, tympanic view; LACM 103975, left: g, cerebral view; h, tympanic view. All natural size.

terior end of the palate, and they extend anteriorly only slightly beyond the level of the antorbital notches. However, they diverge dorsoposteriorly and become enlarged as they ascend into the skull anterior to the nares (Fig. 8b). Such a dorsal expansion of the pterygoid sinus is not common in odontocetes, but does occur also in *Lipotes vexillifer* and *Pontoporia blainvillei*.

The palate is fairly flat for most of its length; not quite as flat as in *Pontoporia blainvillei*, and more deeply fissured medially at the posterior end. Premaxillae appear about mid-length on the palate between the maxillae, from which they are separated by elongate sutures. Progressing anteriorly, the premaxillae occupy increasing amounts of the palatal surface so that near the rostral extremity the medial side of the alveolar row is composed entirely of premaxilla (Fig. 8b). The vomer is exposed on the posterior one-fourth of the palate.

On the posterior part of the rostrum the alveolar rows curve slightly dorsally. Here the surface of the maxilla becomes increasingly porous, except for a band of relatively dense bone extending along the dorsal edge of the alveolar row. The alveoli for the teeth are all approximately 2 mm in diameter. The deepest part of the rostrum is at the proximal end ventral to the antorbital notches. Here it is triangular in cross section with a prominent ventral keel. Anterior to this keel are a pair of palatine foramina in each maxilla on either side of the midline. At the deepest part of the keel lie the triangular palatines, wedged between the maxillae.

Periotic. I have previously (Barnes, 1973a:figs. 2a, b) illustrated a periotic (UCMP 57991) from the San Joaquin Formation, a correlative of the San Diego Formation, and identified it as "*Stenodelphis*" *sternbergi*. Periotics like this one have been reported from the San Diego Formation

(Barnes, 1973a; Deméré, 1981:fig. 5) and more are described here, but none has ever been found in association with a skull of *P. sternbergi* nor of any other species of *Parapontoporia*.

I now assign seven periotics collected from the San Diego Formation to *P. sternbergi* based upon such resemblances to periotics of *Lipotes vexillifer* as: comparable proportions among the different parts of the periotic, pointed anterior process with a separate rugose process on its medial side, a curved crest that extends along the lateral side of the anterior process from its tip to a tuberosity immediately anterior to the groove for the tympanic membrane, a relatively small, slightly concave and grooved articular surface for the bulla on the posterior process, a deep cleft between the anterior process and the cochlear portion of the periotic, and a relatively small, circular internal acoustic meatus. The periotic of *Lipotes vexillifer* (see Brownell and Herald, 1972:pl. 3, figs. 1–6; Kasuya, 1973:pl. 10, figs. 16–20; Zhou, Qian, and Li, 1979:pl. 3, figs. 1–6) differs from that of *P. sternbergi* by being much larger and by having a relatively larger cochlear portion with more rugosities on its cerebral surface and a more circular internal acoustic meatus.

The periotic of *Pontoporia blainvillei* (see Kasuya, 1973:pl. 9, figs. 17, 20–23) is considerably different from those of both of the above species by being very small and by having relatively smaller anterior and posterior processes, a smaller tuberosity anterior to the groove for the tympanic membrane, a more inflated cerebral surface, a distinctive reticulated, etched pattern on the tympanic side of the cochlear portion, and by lacking a process on the medial side of the anterior process.

The periotics of *P. sternbergi* from the San Diego Formation are variable (Fig. 9) in the shape and degree of infla-

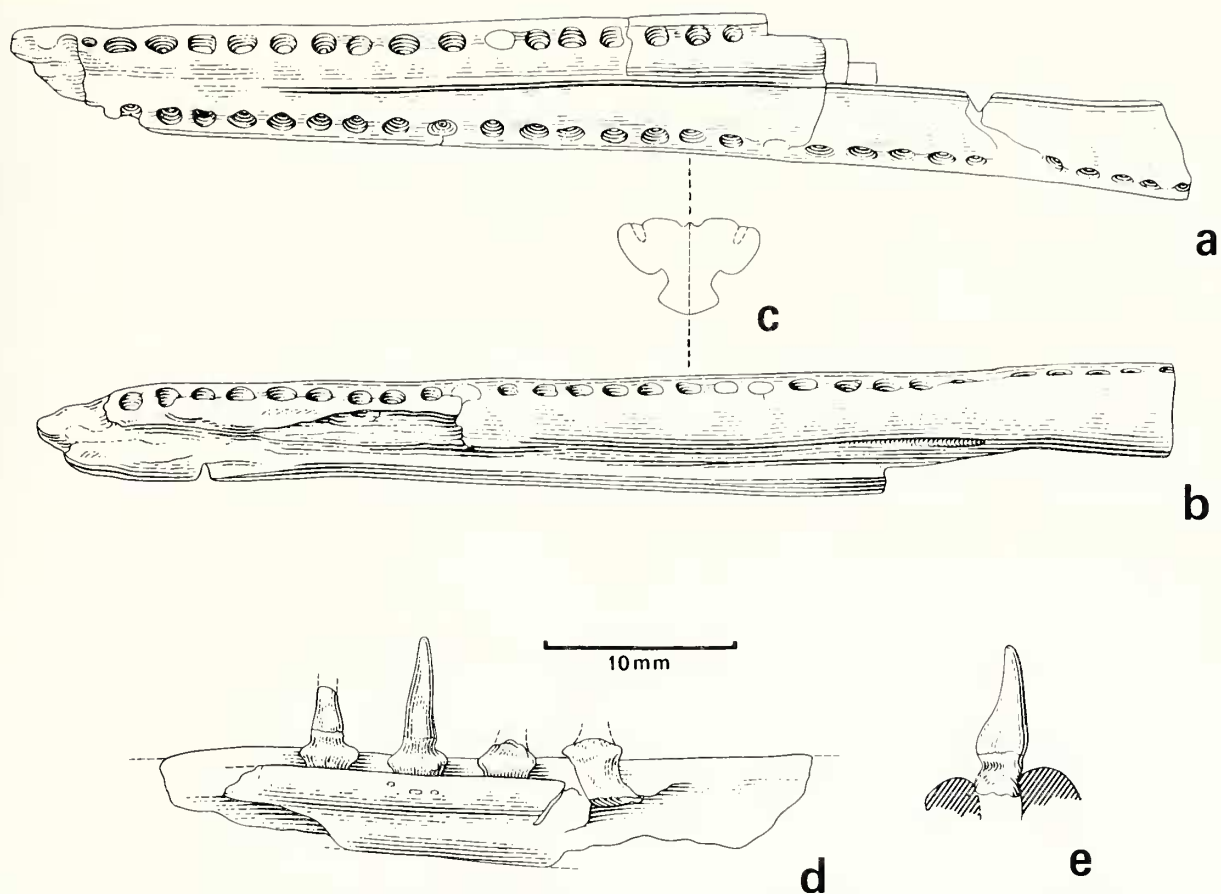


Figure 10. *Parapontoporia sternbergi* (Gregory and Kellogg, 1927), referred specimens from the San Diego Formation: UCMP 88587, mandible fragment: **a**, dorsal view; **b**, left lateral view; **c**, cross section; UCMP 88588, premaxillary fragment with teeth: **d**, lingual view; **e**, posterior view of the complete tooth. Scale line is for Figs. d, e only, Figs. a-c natural size.

tion of the cochlear part and the anterior process, and in the size of the posterior facet for the tympanic bulla.

Mandible. The holotype is a section of a mandible, not a rostrum as it was identified by Gregory and Kellogg (1927). The specimen has no evidence of a vomer or mesorostral gutter which would be present if it were a rostrum, and it is fused at the midline, which is the mandibular symphysis. All skulls of *P. sternbergi*, in a manner typical of odontocetes, exhibit no fusion on the palatal surfaces between the opposite premaxillae or maxillae.

The mandible of *P. sternbergi* is long and slender, and the dentaries are fused for most of their tooth-bearing length by a firm suture. One deep, longitudinal groove extends along the side of each dentary just below mid-height (Fig. 10c). The dorsal margin of this groove projects ventrally so that the opening of the groove is slightly constricted. Anteriorly directed nutrient foramina scattered along the dentary emerge into the upper part of this groove. The groove is less distinct at its posterior end at a point anterior to the end of the symphysis. The ventral surface of the mandible has a broad and flat (or in some specimens a slightly convex) surface and is marked along its midline by a faint groove tracing the position of the mandibular symphysis. The whole surface of

the mandible, including the inside of the longitudinal grooves, is composed of dense, striated bone. Along the midline of the dorsal surface of the symphyseal region of the mandible there is a broad, shallow groove with a slight longitudinal ridge that marks the midline and the position of the mandibular symphysis (Figs. 10a, c). There is no median groove in the mandible of *Pontoporia*. Teeth are set 1 to 2 mm apart in circular alveoli separated by septa of cancellous bone. The alveoli are 2 to 3 mm in diameter.

Teeth. The teeth in the holotype mandible fragment (AMNH 21905) are not typical of those in the sample of specimens now available. Some sort of possibly postmortem mechanical or chemical attrition has reduced the crowns of all the teeth in AMNH 21905 to featureless, rounded cores lacking any enamel (Gregory and Kellogg, 1927:fig. 1). The roots of the teeth are more expanded anteroposteriorly, especially at their apices, than those in any other specimen yet recovered from the San Diego Formation. This is the feature which Gregory and Kellogg (1927:3, fig. 3) described as being like a battle-ax. Because the holotype is larger than the other available mandible fragments, I attribute this exceptional root development to extreme old age of the individual.

Upper and lower teeth are similar in morphology. An un-

worn tooth (Figs. 10d, e) has a crown that is slender, slightly compressed anteroposteriorly, with a nearly straight labial margin and a prominent lingual bulge located proximally near the enamel margin. The enamel is smooth, having no rugosities or crests. No specimen has a complete dentition, but it can be seen in the partial dentitions in the sample available that the more anterior teeth in both the skull and mandible have relatively slender and high crowns, and that progressing posteriorly they are thicker, shorter, and more curved lingually. The anterior teeth are positioned vertically, but the middle and posterior teeth tilt more labially.

The part of the root that is exposed between the bony alveolus and the enamel line of the crown is encircled by a collar which is most prominent anteriorly and posteriorly forming "shoulders" on the root. This condition is preserved on the teeth of the holotype as well. Roots are flattened transversely, particularly so at their apices, which are curved posteriorly (Fig. 10d).

The teeth, or their alveoli, in the nearly complete skull LACM 6238 total at least 77 on each side, and the rostrum was probably at least 20 mm longer when complete. Because the number of teeth in *P. sternbergi* is so close to the known number of 80 to 82 on each side of each jaw in the holotype of *P. pacifica*, I believe that the two species had similar numbers of teeth in both the rostrum and mandible.

***Parapontoporia wilsoni*, new species**

Figures 11–16, 20b, 21a

Stenodelphininae, genus and species new (part): Barnes, 1977: 331.

DIAGNOSIS OF SPECIES. A species of *Parapontoporia* differing from *P. pacifica* by having skull with premaxillae depressed, forming a basin on proximal surface of rostrum anterior to level of antorbital notches; differing from *P. sternbergi* by having facial region longer than wide (antorbital notch to occipital crest versus supraorbital width), deeper basin on proximal surface of rostrum, antorbital process smaller, cranial vertex (comprised of frontals and nasals) lower and less compressed transversely, nares not as vertically oriented in passage through the skull but curving more around anterior wall of braincase, temporal fossa more elongate anteroposteriorly, zygomatic process of squamosal less inclined anteriorly, squamosal between postglenoid process and paroccipital process not as greatly compressed anteroposteriorly; and differing from both *P. sternbergi* and *P. pacifica* by having shorter fossae for pterygoid sinuses on palatines.

HOLOTYPE. UCMP 83790, incomplete skull consisting of the facial portion of the braincase, the posterior part of the rostrum and the basicranium, missing part of basioccipital, supraoccipital, squamosals, pterygoids, parietals, and basisphenoid, collected by John Stanley prior to 1966.

TYPE LOCALITY. UCMP V-6969, in the sea cliff north of Manresa Beach, Santa Cruz County, California.

FORMATION AND AGE. The lower part of the Purisima Formation, latest Miocene, correlated with the "Jacalitos" provisional mega-invertebrate stage of Addicott (1972) and

indirectly with the Hemphillian North American land mammal age, and approximately 6 to 8 million years old. The type locality at Manresa Beach is a considerable, but as yet undetermined distance higher stratigraphically than the base of the Purisima Formation and the type locality of the pin-niped *Dusignathus santacruzensis* Kellogg, 1927. The age of the lower part of the Purisima Formation has been considered by Cummings, Touring, and Brabb (1962) as correlative with the Jacalitos Formation in the San Joaquin Valley, and by Barnes (1977) and Repenning and Tedford (1977) as also correlative with the lower member of the Almejas Formation on Isla Cedros, Baja California, Mexico.

ETYMOLOGY. The species name honors the late Mr. Leslie E. Wilson, who was a teacher, a collector, and researcher of fossil odontocetes, and a generous benefactor to the University of California Museum of Paleontology. Mr. Wilson helped establish the Remington Kellogg Memorial Fund at the Museum to support student research on fossil marine mammals.

DESCRIPTION. The holotype of *P. wilsoni* (Figs. 11–16) may be compared with the entire cranium and the proximal part of the rostrum of *P. sternbergi*, but only the anterior part of its facial region and the proximal part of its rostrum are directly comparable with the holotype of *P. pacifica*. To avoid the repetition that would arise from describing identical structures known for the two previously described species of *Parapontoporia*, those structures that are not known in the others, or those that serve to differentiate *P. wilsoni* from them, will be emphasized in the following text.

The braincase of *P. wilsoni* is more elongate anteroposteriorly than that of *P. sternbergi* (Fig. 21). In *P. wilsoni* the facial region is relatively longer, the cranial vertex is not so steeply peaked, the nares do not pass so steeply into the skull, the temporal fossa is longer anteroposteriorly, and the posterior part of the squamosal, above the mastoid region and between the glenoid fossa and the paroccipital process, is not so compressed in an anteroposterior plane.

The basin that is located in the center of the proximal part of the rostrum is approximately 8 mm deep; nearly twice as deep as it is in *P. sternbergi*. In *P. pacifica*, there is no such basin (Figs. 20a–c). The premaxillary foramina are located approximately 4 mm farther posterior, relative to the antorbital notches, than they are in *P. sternbergi*. Each foramen has the three typical sulci connected with it (anteromedial, posteromedial, and posterolateral), however, the anterior side of the premaxillary foramen and the proximal part of the anteromedial sulcus are roofed over by bone (Fig. 11), even more so than in *P. sternbergi*, in an unusual manner. The posterolateral sulcus is very deeply incised into the premaxilla and its lateral edge is overhung by a sharp lip of bone. Posterior to this, the posterolateral sulcus curves along the lateral edge of the premaxilla and becomes indistinct opposite the posterior edge of the nares.

The posterior ends of the premaxillae are complete on the holotype of *P. wilsoni*, and confirm the previously given description of this area in *P. sternbergi*. The right spiracular plate is wider than the left, and the posterior end of the left premaxilla extends farther posteriorly than the right. Both

premaxillae extend posteriorly closer to the anterolateral corners of the nasals than they do in *P. sternbergi*, and this I interpret as a more primitive character.

The supraorbital region is more complete on the holotype of *P. wilsoni* than it is on any specimens of the other species of *Parapontoporia*, and the antorbital processes and maxillary crests are perfectly preserved. Each antorbital notch is approximately 8 mm deep and, in addition to being partly constricted medially by the maxillary eminence, is partially overlapped laterally by the anterior end of the anteromedially canted maxillary crest on the supraorbital process. The maxillary crests are similar in location, but relatively smaller than those in *Lipotes vexillifer*, *Pliopontos littoralis*, and *Pontoporia blainvillei*. In *Parapontoporia wilsoni*, the apex of the crest forms an uninterrupted arc from the antorbital process to the postorbital process. Its lateral surface is slightly convex and comprised of maxilla as well as of the frontal and lacrimal above the orbit. In *Pontoporia* this crest is similarly shaped, but is higher, narrower, located closer to the premaxilla, and the lateral surface of the crest is rugose, excavated and slopes more medially, and concomitantly, the frontal and lacrimal are more exposed dorsally. The same crest in *Lipotes vexillifer* is developed into more of a knob.

In *Parapontoporia wilsoni* there is a wide fossa in the maxilla medial to the maxillary crest that extends from the antorbital notch posterolaterally toward the postorbital process. The large posterior maxillary foramen is located medial to this depression where the maxillary surface changes its slope and ascends toward the narial region and the cranial vertex.

Compared with *P. sternbergi*, *P. wilsoni* has the following primitive characters. The occipital condyles protrude more prominently from the occipital shield (Figs. 13, 14), the posterior part of the temporal fossa is not roofed over as far laterally by the maxilla and frontal, the paroccipital process is not located as far anteriorly on the braincase and therefore is located less beneath the temporal fossa, and the posterior part of the zygomatic process of the squamosal is not compressed against the paroccipital process and therefore the sternomastoid muscle fossa and the intervening bone that is dorsal to the mastoid process is nearly three times the width. The falcate processes of the basioccipital are thinner and are more excavated laterally for the peribullary sinus than in *P. sternbergi*. This is a derived character. On the holotype of *P. wilsoni*, the falcate process is in many places only 1 to 2 mm thick, and in one place it is so thin that, even in its fossilized state, it will transmit light. The zygomatic process of the squamosal is farther from the braincase wall and the intervening squamosal fossa is therefore wider. The shelf of bone anterior to this fossa is small and not upturned as in *P. sternbergi*. The lateral margin of the glenoid fossa forms a more prominent, vertical border (Figs. 15, 16).

The orbit is small and the frontal forms the posterior two-thirds of its roof. The lacrimal is large compared with species of Delphinidae and forms the anterior one-third of the orbital roof (Fig. 16). In *Pontoporia blainvillei* and *Lipotes vexillifer* the lacrimal is larger yet.

The anterior end of the jugal, as is typical of most modern odontocetes, is fused to the lacrimal, extends anteriorly be-

neath the maxillary eminence on the proximal part of the rostrum and is surrounded dorsally and ventrally by the maxilla. The zygomatic process of the jugal departs from the body of the fused jugal and lacrimal on the anteromedial side of the antorbital notch beneath this eminence. This location of departure of the zygomatic process is similar to that in *Lipotes vexillifer*, but different from that in *Pontoporia blainvillei* in which it is located posterior to the antorbital notch. No known specimen of *Parapontoporia* has a complete jugal.

The optic foramen leaves the braincase beneath a relatively massive strut of bone on the frontal lying posterolateral to the naris. The orbital apertures of the infraorbital foramen complex join to form a large recess in the medial wall of the orbit. These foramina connect dorsally with the maxillary and premaxillary foramina. There is a large but shallow fossa under the anterior part of the supraorbital process indicating that this area held a preorbital lobe of the pterygoid sinus of the middle ear air sinus system.

PHYLOGENETIC RELATIONSHIPS

Before discussing interrelationships of the subfamilies within the family Pontoporiidae, it is important to clarify which previously reputed pontoporiids are not, in my opinion, demonstrably members of the group. *Lonchodelphis occiduus* (Leidy, 1868) is a problematical dolphin from the latest Miocene Purisima Formation in central California. The species was based upon a rostral fragment, and was believed by Allen (1924) to be related to *Pontoporia* after it had been allied first with *Delphinus* by Leidy (1868) and later with *Phocoena* by Jordan and Gilbert (1919). I have (Barnes, 1977:332; 1984:12) pointed out that the specimen is not similar to any specimen of a pontoporiid. No other specimens have ever been assigned to the species and, until a more complete specimen is identified, it should be considered as some unknown type of odontocete. Simpson (1945:101) classified in the Stenodelphininae the Pliocene age Argentinian species, *Pontivaga fischeri* Ameghino, 1891, which was based on a lower jaw fragment. The species cannot be objectively compared with another, contemporaneous pontoporiid from Argentina, *Pontistes rectifrons* Burmeister, 1885, however, which was based on a skull (see Barnes, 1984:11, 12). de Muizon (1983) suggested that the Late Pliocene age Peruvian species, *Pliopontos littoralis* was very closely related to Recent *Pontoporia blainvillei* and might have evolved from *Pontistes rectifrons*. I accept the idea that *Pontoporia*, *Pontistes*, and *Pliopontos* are related, and *Pontivaga* must be considered as an odontocete of uncertain affinities until a mandible of *Pontistes rectifrons* has been compared with it.

In the classification I propose here, the family Pontoporiidae includes three subfamilies. The nominate subfamily Pontoporiinae includes Recent *Pontoporia blainvillei*, the closely related Pliocene Peruvian *Pliopontos littoralis* de Muizon, 1983, and the Pliocene Argentinian species, *Pontistes rectifrons* Burmeister, 1885. These species all have symmetrical cranial vertices. *Parapontoporia*, the sole genus in the subfamily Parapontoporiinae, has teeth, rostrum, and some cranial characters like *Pontoporia*, but has an asym-

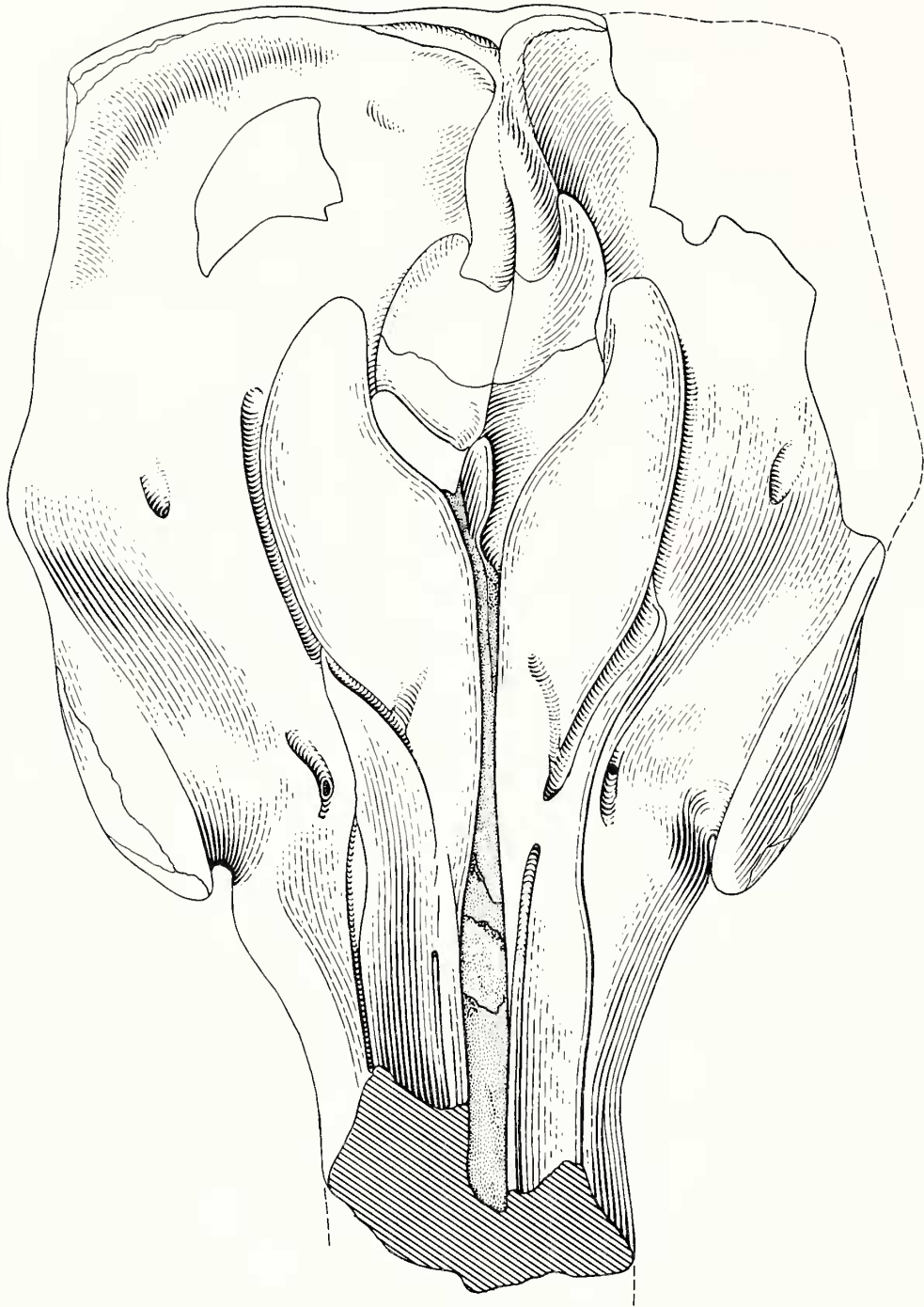


Figure 11. *Parapontoporia wilsoni*, new species, holotype, UCMP 83790, partial skull, dorsal view, natural size.

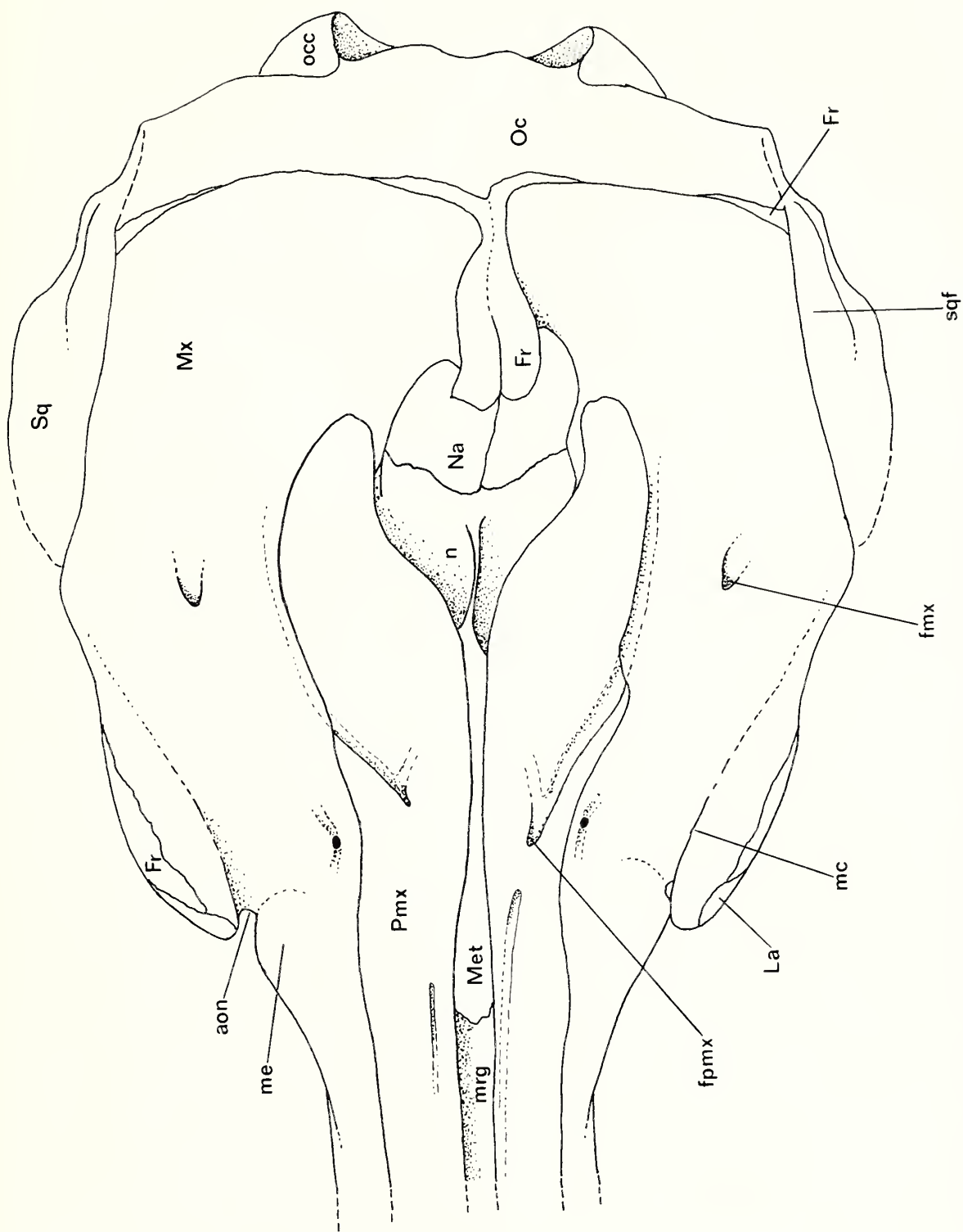


Figure 12. *Parapontoporia wilsoni*, new species, restoration of partial skull based on holotype, UCM 83790, dorsal view, natural size.

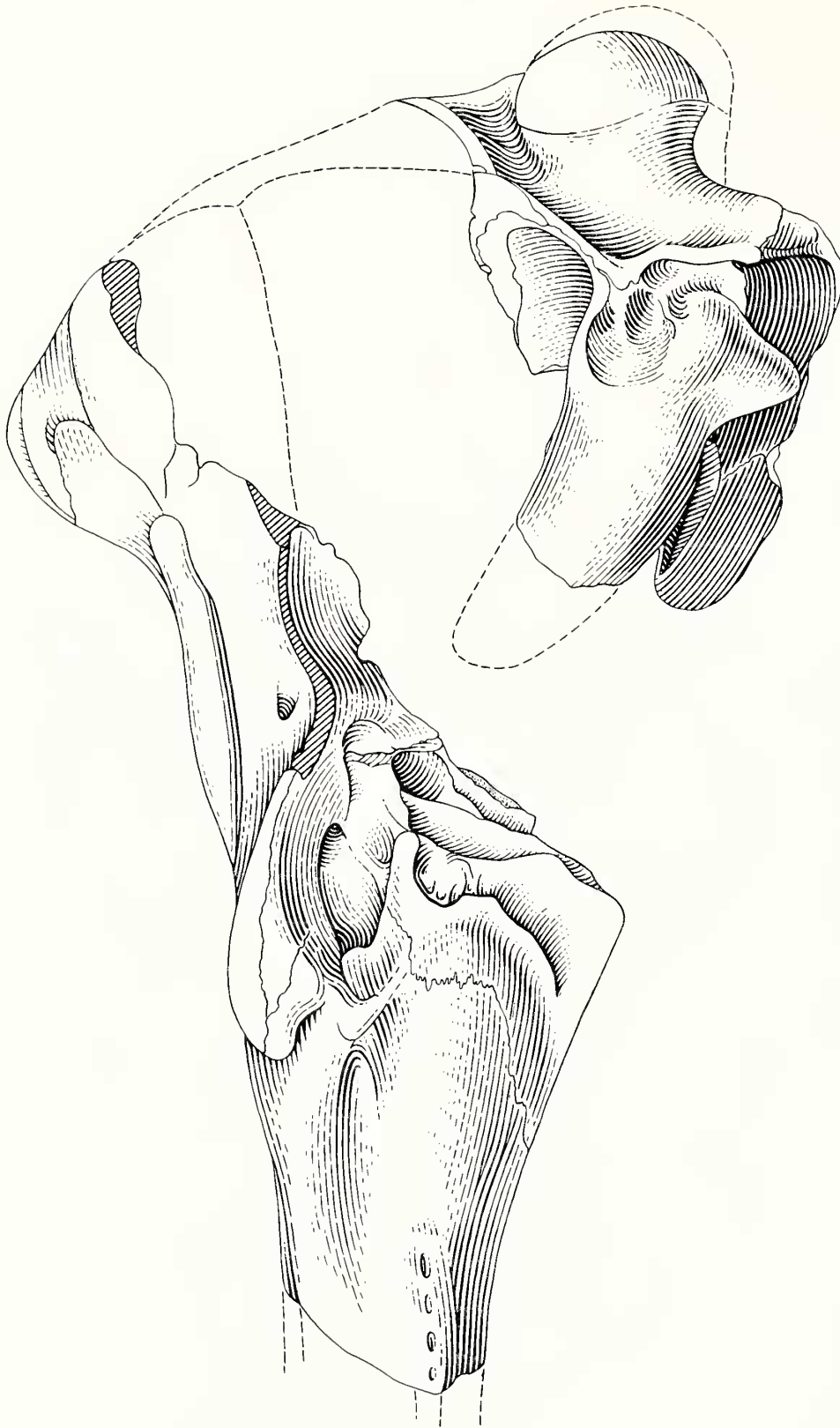


Figure 13. *Parapontoporia wilsoni*, new species, holotype, UCMMP 83790, partial skull, left lateral view, natural size.

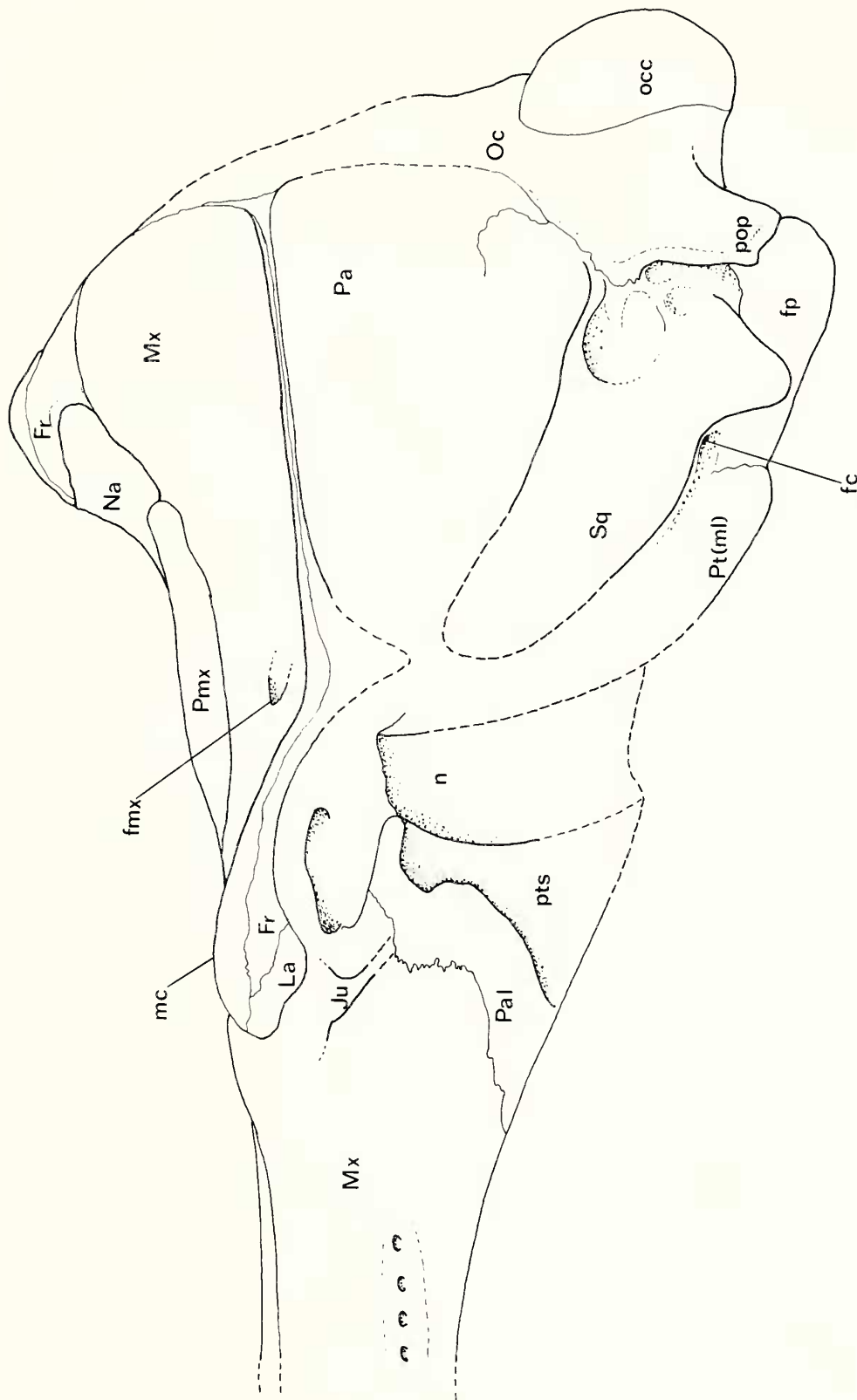


Figure 14. *Parapontoporia wilsoni*, new species, restoration of partial skull based on holotype, UCMP 83790, left lateral view, natural size.

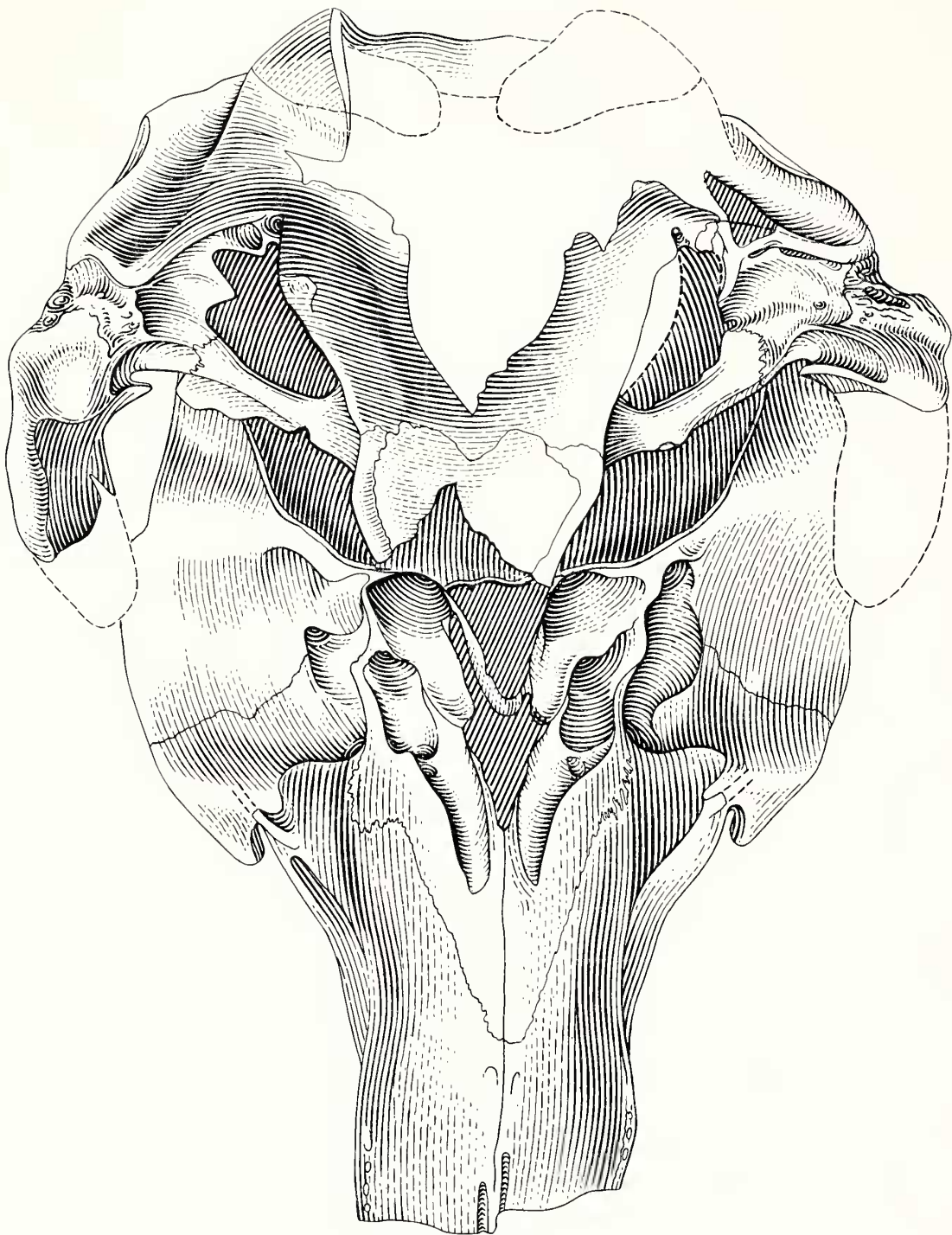


Figure 15. *Parapontoporia wilsoni*, new species, holotype, UCMMP 83790, partial skull, ventral view, natural size.

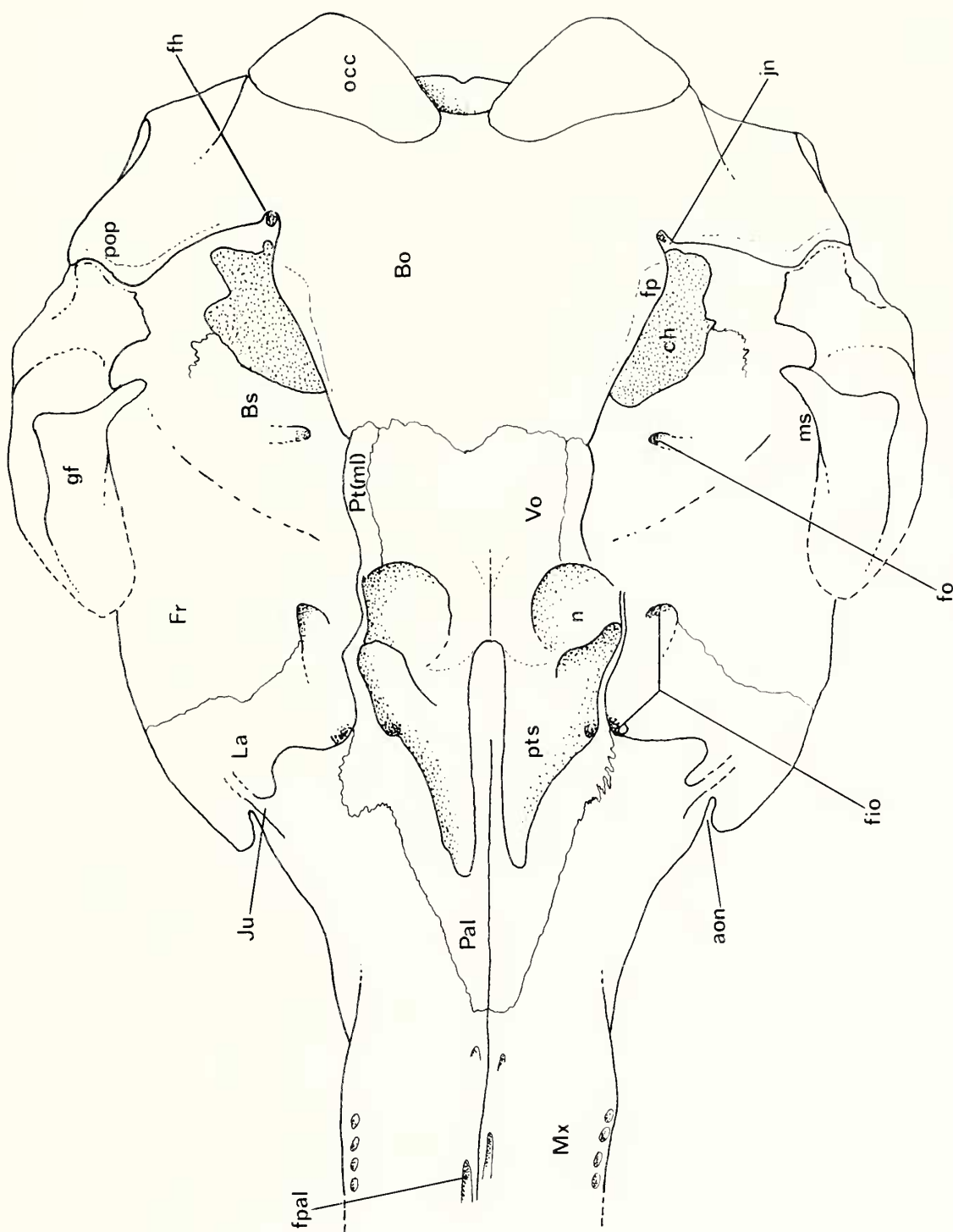


Figure 16. *Parapontoporia wilsoni*, new species, restoration of partial skull based on holotype, UCMMP 83790, ventral view, natural size.

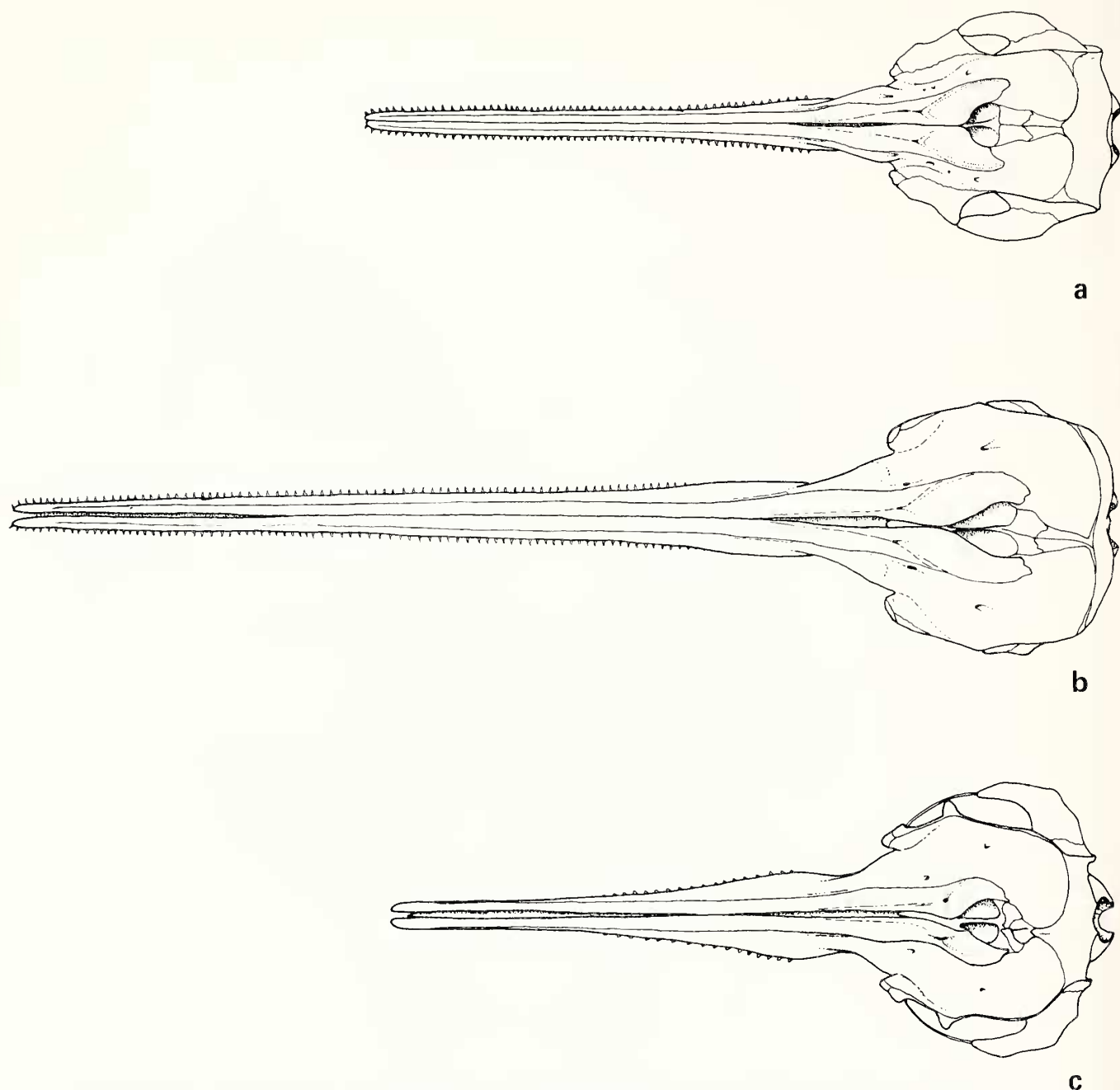


Figure 17. Skulls of Pontoporiidae: **a**, *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844); **b**, *Parapontoporia sternbergi* (Gregory and Kellogg, 1927); **c**, *Lipotes vexillifer* Miller, 1918. (**a** after Flower, 1869:pl. 28, fig. 3; **b** after Fig. 7b, this paper; **c** after Brownell and Herald, 1972:fig. 1.)

metrical cranial vertex and some other derived cranial characters like *Lipotes*. *Parapontoporia*, therefore, is in many ways intermediate between *Pontoporia* and *Lipotes*. The latter was designated by Zhou, Qian, and Li (1979) as the type genus of a new family, the Lipotidae. To reflect the close relationships and to balance the classification, I recognize the Lipotinae as a third subfamily of Pontoporiidae.

Zhou, Zhou, and Zhao (1984) described a fossil that is

possibly Miocene in age as an extinct member of the Lipotidae, calling it *Prolipotes yujiangensis*. All that is known of the species is the holotype mandible fragment, but the specimen does have morphology very similar to the extant *Lipotes vexillifer*. Odontocete mandibles generally have fewer diagnostic characters than do skulls, and as a rule it is unwise to make taxonomic inferences from them. There is nothing in the morphology of *P. yujiangensis*, however, that would

preclude a possible relationship between it and *L. vexillifer*, and I provisionally classify both species in the same subfamily.

In summary, the family Pontoporiidae includes three subfamilies: the Pontoporiinae containing *Pontoporia blainvillei* and extinct taxa (*Pontistes rectifrons*, *Pliopontos littoralis*) that have symmetrical crania, very long rostra, and extreme polydonta; the Parapontoporiinae including species of *Parapontoporia*, which have asymmetrical crania, very long rostra, and extreme polydonta; and the Lipotinae including *Lipotes vexillifer*, which has an asymmetrical cranium, shorter rostrum, and only moderate polydonta (Fig. 17). The fossil *Prolipotes yuijiangensis* may belong to the latter subfamily, but no cranial material is known that could confirm this. The family Pontoporiidae is united by a unique suite of shared derived characters as given in the family diagnosis.

The deep grooves on the lateral sides of the dentaries in fossil *Parapontoporia sternbergi* and Recent *Pontoporia blainvillei* are convergent derived characters (autapomorphies). I base this conclusion on two lines of evidence. (1) The most primitive, and chronologically oldest species of the genus *Parapontoporia*, *P. pacifica*, has no mandibular grooves. Instead it has a shallow longitudinal sulcus on each dentary. Deep mandibular grooves are present, however, in the chronologically youngest species, *P. sternbergi* (Figs. 20d, e). (2) Each dentary of Recent *Pontoporia blainvillei* has only one mental foramen in the mandibular groove, and this enters the groove at its posterior end. In *Parapontoporia* each dentary has four or five foramina that are spaced out along the length of the mandible. This is the case in species of *Parapontoporia* both with and without a mandibular groove, and is the primitive (plesiomorphic) condition among odontocetes.

In *Pontoporia blainvillei*, and apparently also in *Parapontoporia sternbergi*, the nerves and blood vessels emerging from the mental foramina would lie in these grooves, and presumably derive some measure of protection from them. Therefore, the function of the mandibular grooves is the same in both genera, but their origins are separate.

I believe that the unique features of the teeth of *Pontoporia blainvillei* and *Parapontoporia* spp. are shared derived (synapomorphic) characters because even the earliest species of *Parapontoporia*, *P. pacifica*, has them. The rugose texture of the enamel on the teeth of *Lipotes vexillifer* and *Prolipotes yuijiangensis* is probably a primitive character. Many primitive odontocetes have rugose enamel, and this I regard as a carryover from earlier squalodonts and agorophiids. Most modern species have smooth enamel, the derived condition. *Inia geoffrensis*, often classified with *Lipotes vexillifer* in earlier works, has rugose enamel, but the posterior teeth have very large lingual shelves and the dentition is otherwise not very much like that of *Lipotes vexillifer*. Teeth of both *Lipotes vexillifer* and *Prolipotes yuijiangensis* have a slightly swollen shoulder on the root, and this is a derived character that is shared with *Pontoporia blainvillei* and *Parapontoporia* spp.

An asymmetrical cranial vertex that is offset to the left side is a convergent derived character that has appeared sep-

arately in different groups of odontocetes at different times. Prior to Late Miocene time, representatives of most odontocete families, with the exception of such groups as sperm whales (Physeteridae) and beaked whales (Ziphiidae), had symmetrical cranial vertices and narial regions. *Lipotes vexillifer* and *Parapontoporia* spp. have, among other shared, derived cranial characters, asymmetrical cranial vertices and asymmetrical bones around the external nares. The cranial vertices of *Pontoporia blainvillei* and the fossil species of Pontoporiinae, however, are symmetrical, as well as being lower and more elongate anteroposteriorly than those of *Parapontoporia* spp. or *Lipotes vexillifer*. Because *Pontoporia blainvillei* has asymmetrical nasal diverticula (Schenkken, 1972) and because so many of its other features are derived, I suspect that its cranial symmetry is not primitive, but is a reversal from an earlier asymmetrical condition.

If the above arguments are accepted as valid and *Pontoporia*, *Parapontoporia*, and *Lipotes* are indeed closely related, then there are at least two possible diagrams that would show their interrelationships, depending on which of the above characters are considered to be shared and derived versus convergent and derived.

In the most parsimonious scheme, and the one that I prefer (Fig. 18), the similar structures of the teeth of *Parapontoporia* and *Pontoporia* are interpreted as shared derived characters (synapomorphies) and the deep mandibular grooves as convergent derived characters (autapomorphies). The asymmetrical cranial vertex of *Parapontoporia* spp. and *Lipotes vexillifer*, while being a derived character relative to more primitive odontocetes, is the shared primitive character state (symplesiomorphy) for Pontoporiidae, and the symmetrical cranial vertex of *Pontoporia* (and fossil Pontoporiinae) is a unique derived character (autapomorphy), being secondarily symmetrical and a reversal from the asymmetrical condition.

Another possible interpretation of relationships (Fig. 19) is one in which the symmetrical cranial vertex of *Pontoporia blainvillei* is considered to be primitive for the family, and the asymmetrical vertices of *Parapontoporia* spp. and *Lipotes vexillifer* are shared derived characters. This is more consistent with traditional ideas about acquisition of cranial asymmetry in odontocete families, but requires an assumption that in addition to deep mandibular grooves being convergent, as in the first case above, that the unusual *Pontoporia*-like teeth and the very long rostrum are the primitive character state for Pontoporiidae. In that case the lesser tooth count, thick, short rostrum and mandible, and rugose tooth enamel of *Lipotes vexillifer* are derived characters and all of these would then necessarily be interpreted as secondary reversals back to the primitive odontocete condition. In each of the two possible schemes of relationships discussed above, the intermediate position of *Parapontoporia* spp. and the polarity of characters and inferred interrelationships of its included species remain unchanged.

Within the genus *Parapontoporia*, the most primitive species is Late Miocene *P. pacifica*, with no mandibular grooves and no rostral basin (Figs. 20a, d). The approximately contemporaneous species, *P. wilsoni*, however, is more derived and has a very deep rostral basin (apomorphy), but

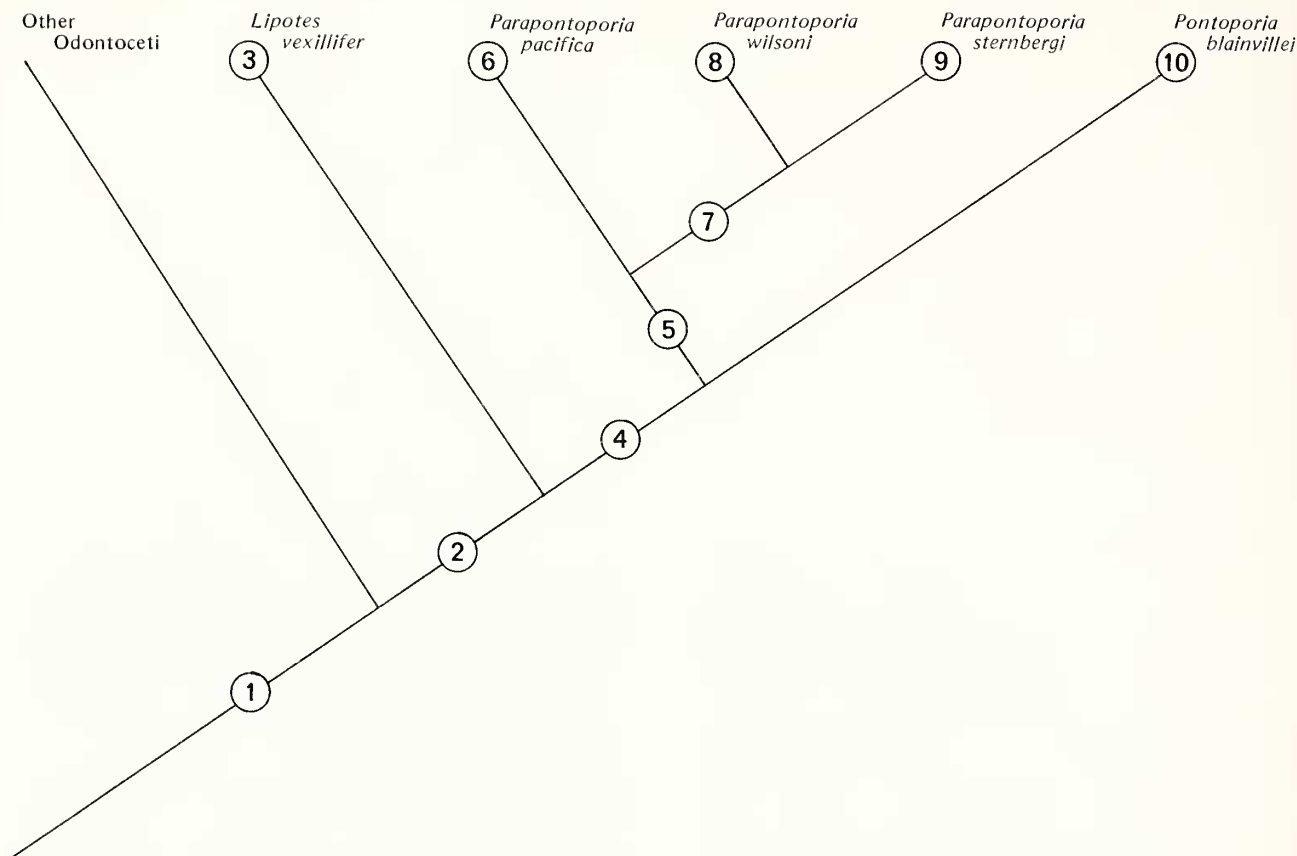


Figure 18. Diagram of the most parsimonious scheme of relationships among taxa of Pontoporiidae, with the fewest implied convergences and evolutionary reversals, but requiring the assumption that the cranial symmetry of *Pontoporia blainvillei* is the result of a secondary reversal from an earlier asymmetrical condition, a contradiction to traditional ideas regarding odontocete evolution. Characters marking the dichotomies are as follows: (1) The primitive state for Odontoceti is a symmetrical cranial vertex. (2) An asymmetrical cranial vertex (apomorphy) is presumed to be the primitive character state of the earliest members of the Pontoporiidae. The family is differentiated from all other groups of Odontoceti, including all other families within the superfamily Platanistoidea, by the shared characters given in the family diagnosis. Interrelationships of the other platanistoid families are insufficiently understood, within the context of the analysis presented here, to be shown separately in this scheme. (3) *Lipotes vexillifer* retains a relatively short, thick rostrum and mandible, and rugose enamel on the teeth as primitive characters (subfamily Lipotinae, presumably including *Prolipotes yujiangensis*, but the species is insufficiently known to include on the diagram). (4) *Parapontoporia* and *Pontoporia* share as synapomorphies: polydonta, *Pontoporia*-like teeth, extremely long rostrum and mandible, and a bony wall in the orbit formed by a posterior extension of the lateral lamina of the pterygoid and, at least in part, also by posterior extensions of the palatine and maxilla. These characters are shared by the subfamilies Parapontoporiinae and Pontoporiinae. (5) Exceptionally long rostrum, extreme polydonta (80–82 teeth in each side of each jaw in contrast with 48–61 in *Pontoporia blainvillei*) are autapomorphies for the genus *Parapontoporia* (subfamily Parapontoporiinae). (6) The most primitive species in the genus. (7) Basin formed on the proximal part of the rostrum; a derived character shared by *P. wilsoni* and *P. sternbergi*. (8) Very deep rostral basin (autapomorphy), otherwise more primitive than *P. sternbergi*, especially in having a braincase that is less foreshortened anteroposteriorly (less telescoped). (9) Anteroposteriorly compressed (more telescoped) cranium, more vertical narial passages, more elevated and more transversely compressed cranial vertex, and deep mandibular grooves are autapomorphies of *P. sternbergi*. The rostral basin is shallower than in *P. wilsoni*, and in this regard *P. sternbergi* is more primitive. (10) *Pontoporia blainvillei* has the following autapomorphies: vomer not exposed on palate, spiracular plates convex and elevated, posterior premaxillary terminations shortened, shallow squamosal fossa between zygomatic process of squamosal and braincase. Where preserved, these characters are also present in the fossil species, *Pontistes rectifrons* and *Pliopontos littoralis*, but the scope of this study does not include a more detailed analysis of the relationships of the latter species (subfamily Pontoporiinae).

a mandible has not been found and it is not known whether or not it had lateral grooves (Fig. 20b). These two species represent two lines of descent within the genus. The much younger species, the Late Pliocene *P. sternbergi*, has deep mandibular grooves (apomorphy), but only a shallow rostral basin (Figs. 20c, e). Morphologically and temporally it could

have evolved from *P. pacifica*. It would have had to have undergone an evolutionary reversal, a shallowing of the rostral basin, to have evolved from *P. wilsoni*. The braincase of *P. sternbergi* is anteroposteriorly compressed (apomorphy) when compared with that of *P. wilsoni* (Fig. 21). Because *P. pacifica* is so primitive, it undoubtedly had an anteroposte-

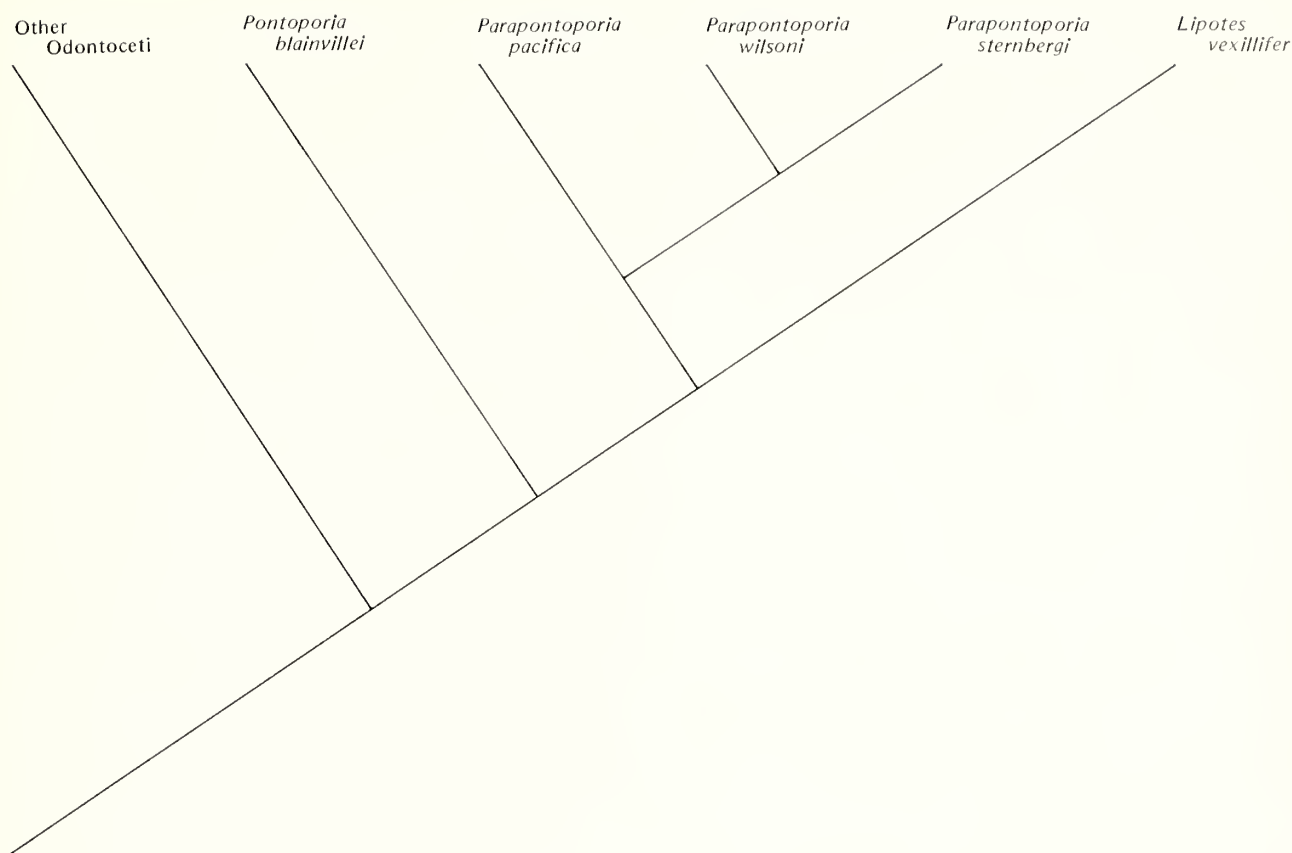


Figure 19. An alternative, less parsimonious interpretation of relationships among taxa of Pontoporiidae. In this scheme the symmetrical cranial vertex of *Pontoporia blainvillei* would be considered as the primitive character state for the family Pontoporiidae, as it is for primitive odontocetes, and the asymmetrical cranial vertices of *Parapontoporia* spp. and *Lipotes vexillifer* would be synapomorphic. This arrangement would suggest, however, that many other characters were the result of convergent evolution of derived states (e.g., long rostra, mandibular grooves, polydonta, and the *Pontoporia*-like teeth in *Pontoporia blainvillei* and *Parapontoporia* spp.) or of evolutionary reversals back to primitive states (e.g., short rostrum, low tooth count, and rugose enamel on teeth of *Lipotes vexillifer*).

riorly elongate braincase with proportions like that of *P. wilsoni*, and if *P. pacifica* were ancestral to *P. sternbergi*, such anteroposterior compression could plausibly have occurred within the lineage in the elapsed time interval of several millions of years.

CLASSIFICATION

Class Mammalia Linnaeus, 1758

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Superfamily Platanistoidea (Gray, 1863) Simpson, 1945

Family Pontoporiidae (Gill, 1871) Kasuya, 1973

Subfamily Lipotinae (Zhou, Qian, and Li, 1979),
NEW RANK AND CONTEXT

Prolipotes Zhou, Zhou, and Zhao, 1984

Prolipotes yujiangensis Zhou, Zhou, and
Zhao, 1984. ?Miocene, China

Lipotes Miller, 1918

Lipotes vexillifer Miller, 1918. Recent, China

Subfamily Parapontoporiinae Barnes, 1984

Parapontoporia Barnes, 1984

Parapontoporia pacifica Barnes, 1984. Latest
Miocene, Baja California

Parapontoporia wilsoni, NEW SPECIES.
Latest Miocene, California

Parapontoporia sternbergi (Gregory and Kellogg, 1927). Late Pliocene, California

Subfamily Pontoporiinae (Gill, 1871) Barnes, 1984

Pontistes Burmeister, 1885

Pontistes rectifrons (Bravard, 1884). Pliocene, Argentina

Pliopontos de Muizon, 1983

Pliopontos littoralis de Muizon, 1983. Early
Pliocene, Peru

Pontoporia Gray, 1846

Pontoporia blainvillei (Gervais and d'Orbigny, 1844). Recent, Atlantic coast of South America

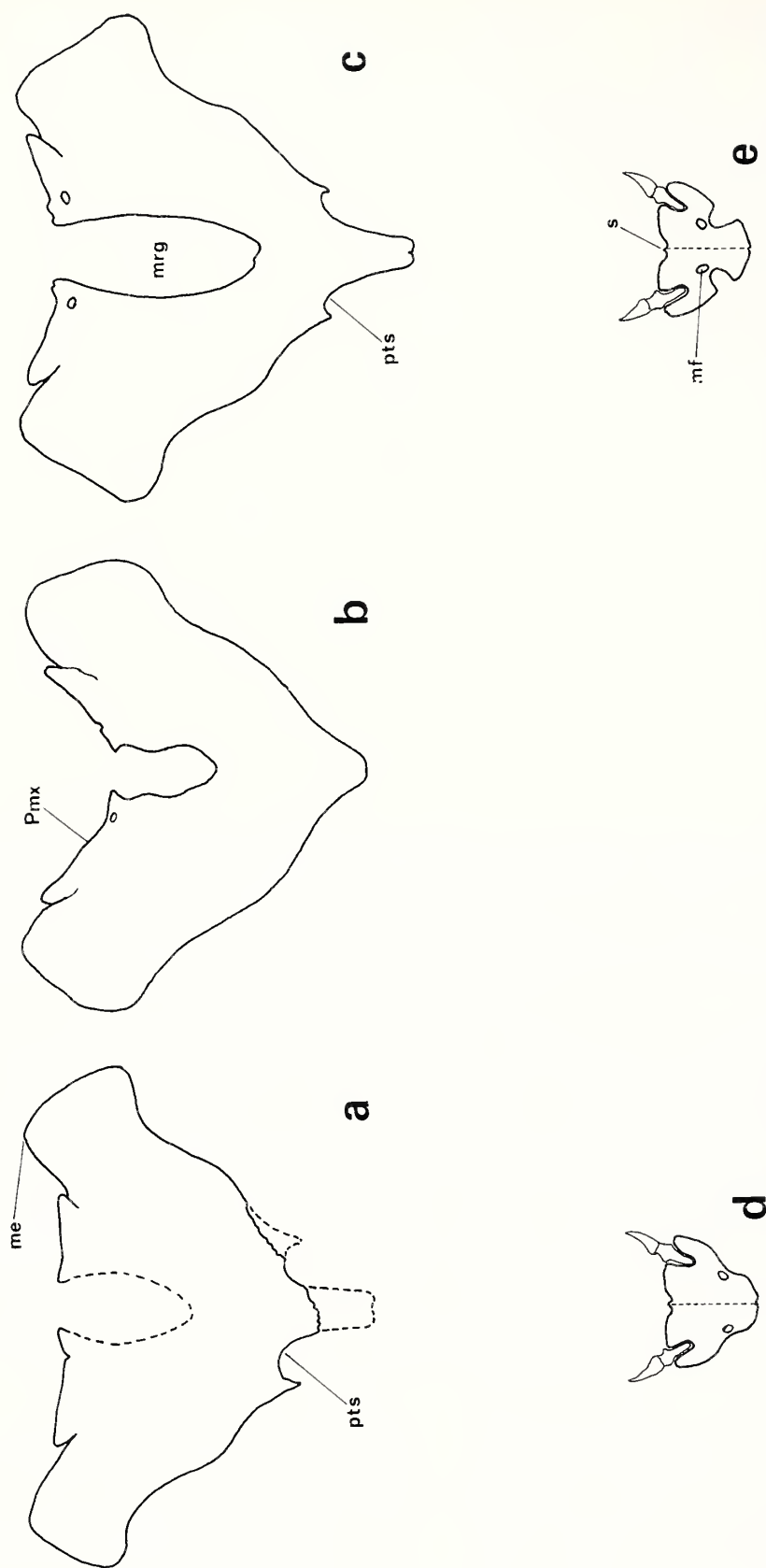


Figure 20. Comparisons of cross sections through the proximal part of the rostrum of **a**, *Parapontoporia pacifica* Barnes, 1984; **b**, *P. wilsoni*, new species; **c**, *P. sternbergi* (Gregory and Kellogg, 1927); and through mandibles at mid-length of the symphyseal area of **d**, *P. pacifica*; and **e**, *P. sternbergi*; all natural size.

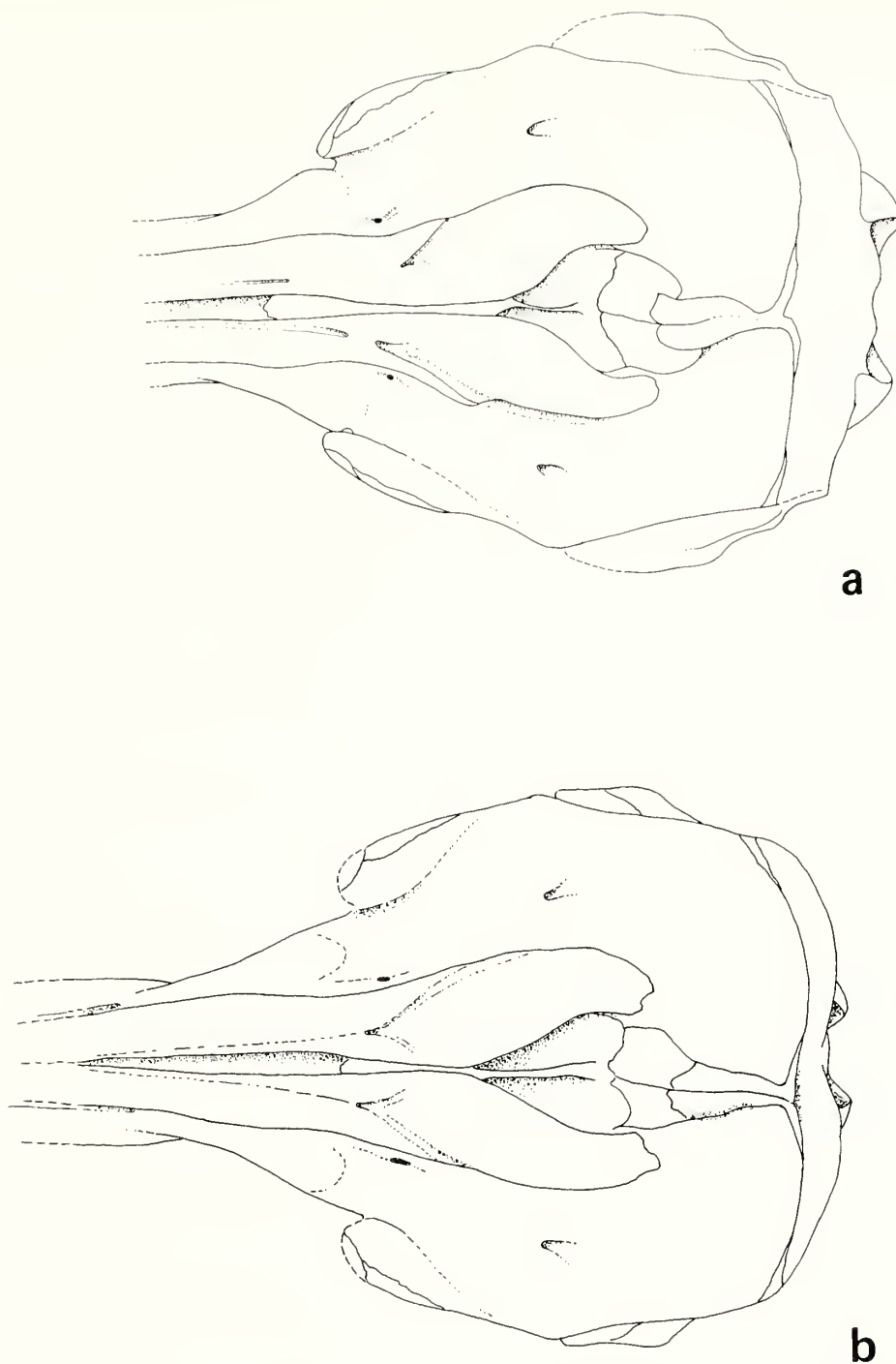


Figure 21. Dorsal views of braincases of two species of *Parapontoporia*; **a**, *P. wilsoni*, new species, based on the holotype; **b**, *P. sternbergi* (Gregory and Kellogg, 1927), based on referred specimens, principally LACM 6238; reduced to the same cranium length.

Use of either of two family group names, Pontoporiidae (or Pontoporiinae) and Stenodelphininae (incorrectly emended to Stenodelphininae), has varied among authors, depending, in some cases, upon their acceptance or rejection of the notion that *Pontoporia* Gray, 1846, is a valid senior synonym of the genus name *Stenodelphis* d'Orbigny and Gervais, 1847.

Especially during the early 1900's it was understood by many authors that *Pontoporia* was a preoccupied name, and *Stenodelphis* was the preferred usage. More recently, *Pontoporia* has been confirmed as valid (Hershkovitz, 1961), and in recent literature is the commonly used generic name.

The family group name based upon *Pontoporia*, Ponto-

poriidae, is available from Gill's (1871) first use of Pontoporiinae as a monotypic subfamily of the Platanistidae. The following year Gill (1872) reclassified the Pontoporiinae as a subfamily in the family Delphinidae. Gray (1871) used the incorrectly formed family name Pontoporiadae, which he classified in the suborder Delphinoidea with the families Iniidae, Delphinidae (including phocoenids), Grampidae, Globicephalidae, Orcadae (*sic*) (these latter three are now classified as synonyms of Delphinidae), and Belugidae (correctly called Monodontidae). True (1908) recognized the genus name *Stenodelphis* instead of *Pontoporia*, and therefore proposed the subfamily Stenodelphininae which he classified in the family Delphinidae. He was followed in this by Miller (1923), Kellogg (1928), and many subsequent authors, including myself (Barnes, 1977), who, however, employed the incorrectly emended form of the name, Stenodelphininae. Simpson (1945) used the same incorrectly formed name, but classified the subfamily with the subfamilies Iniinae and Platanistinae in the family Platanistidae. Rice (1967) recognized the same hierarchy and ranks as did Simpson, but substituted the earlier and correct name, Pontoporiinae. Kasuya (1973) used Gill's name at the family rank, Pontoporiidae, and he classified the family in the superfamily Plantanoidea, in which he also included the families Iniidae (including *Lipotes*) and Platanistidae. Zhou, Qian, and Li (1979) erected the new monotypic family Lipotidae for *Lipotes*, which had previously been classified in either Iniidae or Iniinae, and Zhou (1982) classified Lipotidae, Iniidae, Pontoporiidae, and Platanistidae as four separate families in the superfamily Plantanoidea.

In summary, each of the living genera, *Pontoporia*, *Lipotes*, *Inia*, and *Platanista*, has been the basis for establishment of a family group name. Their ranks in published classifications have varied between subfamily and family, and they have usually been classified in the family Platanistidae or the superfamily Plantanoidea correspondingly. *Pontoporia* has also commonly been classified in Delphinidae, and *Lipotes* and *Inia* have usually been classified together in the family Iniidae or subfamily Iniinae. In my classification *Lipotes* is related to *Pontoporia* and classified in the Pontoporiidae, not the Iniidae and Platanistidae are, therefore, separate families.

CONCLUSIONS

The Parapontoporiinae are an extinct Late Miocene and Pliocene eastern North Pacific subfamily of the dolphin family Pontoporiidae and are represented by one genus, *Parapontoporia* Barnes, 1984. This extremely long-snouted genus is morphologically and zoogeographically intermediate between the living marine franciscana or La Plata dolphin, *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844), of the southwest Atlantic and the living freshwater beiji or white flag dolphin, *Lipotes vexillifer* Miller, 1918, of China. The latter two are each placed in separate subfamilies of the Pontoporiidae, called the Pontoporiinae and Lipotinae, respectively. There is a possible fossil relative of *Lipotes* Miller, 1918, *Prolipotes yuiangensis* Zhou, Zhou, and Zhao, 1984, of questionable Miocene age from China. Two South Amer-

ican Pliocene fossil species, *Pontistes rectifrons* (Bravard, 1884) and *Pliopontos littoralis* de Muizon, 1983, are related to *Pontoporia*. *Lipotes* had previously been classified in the Iniidae, or more recently put in its own monotypic family, Lipotidae.

The genus *Parapontoporia* has been documented previously by several published references to fossils from the latitudes between approximately 27° and 38° north in California and Baja California under such identifications as *Stenodelphis* (or "*Stenodelphis*") *sternbergi* Gregory and Kellogg, 1927. Among these scattered records are at least three species, each of which is characterized and diagnosed in the present study.

The oldest and most primitive of these is *Parapontoporia pacifica* Barnes, 1984, from the latest Miocene age lower member of the Almejas Formation on Isla Cedros, Baja California, and which is between approximately 6 and 8 million years old. An approximately contemporaneous species, *Parapontoporia wilsoni*, new species, from low in the Purisima Formation in central California differs from *P. pacifica* notably by having a deep basin on the proximal surface of the rostrum. A much younger species from the Late Pliocene age lower member of the San Diego Formation at San Diego, California, *P. sternbergi* (Gregory and Kellogg, 1927), is between approximately 2 and 4 million years old. This species does not have as deep a rostral basin as *P. wilsoni* and has a more anteroposteriorly compressed braincase. It also has deep mandibular grooves that are not present in *P. pacifica*. The species is the most abundantly represented of the three, and is the only one known by a complete skull.

At least two schemes of interrelationships are possible between Lipotinae, Parapontoporiinae, and Pontoporiinae, each of which would require the assumption that reversals have occurred in the evolution of certain characters. The most parsimonious hypothesis is that *Lipotes* is the most primitive, that *Pontoporia* is the most derived, and that *Parapontoporia* is intermediate between them. This would indicate that *Pontoporia* had secondarily acquired a symmetrical cranial vertex, that the asymmetrical cranial vertices of *Lipotes* and *Parapontoporia* are a shared primitive character for the family and that the unusual teeth of *Parapontoporia* and *Pontoporia* are shared and derived. In this case the rugose enamel on the teeth and the shorter and thicker rostrum and mandible of *Lipotes* would be primitive characters, and the deep mandibular grooves of living *Pontoporia blainvillei* and the Late Pliocene fossil *Parapontoporia sternbergi* are convergent and derived.

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